A TEXTBOOK OF BOTANY

REVISED

VOLUME TWO

PHYSIOLOGY

COULTER — BARNES — COWLES

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A TEXTBOOK *of* BOTANY

FOR COLLEGES AND UNIVERSITIES

By

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VOLUME TWO. PHYSIOLOGY

REVISED AND ENLARGED

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PREFACE

THE study of plants may be approached from so many points of view that every laboratory has developed its own method of undergraduate instruction. No laboratory attempts to include all the phases of work that may be regarded as belonging to botany; and therefore each one selects the material and the point of view that seem to it to be the most appropriate for its own purpose. For many years the Hull Botanical Laboratory at the University of Chicago has been developing its undergraduate instruction in botany to meet its own needs. Freed from the necessity of laying special stress upon the economic aspects of the subject, and compelled to prepare students for investigation, it seemed clear that its selection must include the fundamental facts and principles of the science. Its endeavor has been to help the student to build up a coherent and substantial body of knowledge, and to develop an attitude of mind that will enable him to grapple with any botanical situation, whether it be teaching or investigation. It has been thought useful to present this point of view in the present volume. The material of course is common to all laboratories, but its selection, its organization, and its presentation bear the marks of individual judgment.

The three volumes of this series represent three of the general divisions of the subject as organized at the Hull Botanical Laboratory. They are felt to be the more fundamental divisions which should underlie the work of most subdivisions of botanical investigation. For example, a study of the very important subject of plant pathology must presuppose the fundamentals of morphology and physiology; paleobotany is, in part, the application of morphology and ecology to fossil plants; and scientific plant breeding rests upon the foundations laid by morphology, physiology, and ecology. In our selection for undergraduate instruction, therefore, we believe that there has been included the essential foundation for most of the varied work that is included to-day under botany.

We recognize that the presentation of the three subjects here included is very compact, but the books are not intended for reading and recitation. The teacher is expected to use them for suggestive material and for organization; the student is expected to use them in relating his observations to one another and to the general points of view that the books seek to develop. There is a continuity of presentation in each book. Random selection of material might miss the largest meaning. For example, in the part on morphology, the thread upon which the facts are strung is the evolution of the plant kingdom, and each plant introduced has its peculiar application in illustrating some phase of this evolution. When certain unconnected groups are selected for laboratory study, therefore, the intervening text should be read.

It is important to emphasize the fact that the book has been prepared for the use of undergraduate students. It does not represent our conception of graduate work, which should include much that is omitted here. For example, the graduate student should make much larger use of original sources of information, which would involve an extensive citation of literature far beyond the needs of the undergraduate. Still less have these books been written for our professional colleagues, who will notice what they may regard as glaring omissions. Such omissions must be taken to express a deliberate judgment as to what may be omitted with the least damage to the undergraduate student. The motive is to develop certain general conceptions that are felt to be fundamental, rather than to present an encyclopedic collection of facts. This purpose has demanded occasionally also a greater apparent rigidity of form in general statements than is absolutely consistent with all the facts. In presenting the material to students who had not yet developed perspective, it was necessary to choose between a clear and important conception on the one hand, and a contradiction of large truths by isolated facts on the other, which might result in confusion. For the same reasons, the extensive terminology of the subject has been kept in the background as much as possible. Definitions usually are made an incident to the necessary introduction of terms. It is assumed that in so far as the definite application of a term may not seem clear, the student will find a compact definition in the current dictionaries.

For the benefit of the teacher and of our professional colleagues, it should be stated that much attention has been given to the avoidance

of any phraseology that might involve a teleological implication. It has not been possible to avoid such phrases in all cases without introducing clumsiness of expression or breaking the continuity of some important series of structures or events. It should be kept in mind, therefore, that all teleological implications of language that remain are disavowed.

It seems hardly necessary to say that most of the material presented in the book has been worked over by classes repeatedly. Some new matter has been developed incidentally in all the parts in connection with ordinary laboratory and field work. Especially in Volume II many scattered observations and some new points of view have been included. There has been no intention to include any formal contribution, but merely to present in general outline some of the material worked over by undergraduates, some of the results of investigation already published in contributions from the laboratory, and some observations and conclusions that hardly seem to justify separate publication. Provision has been made for students with more interest or more time than usual to get a somewhat larger view, by including in smaller type further details of structure, additional illustrative material, and suggestive theories. The selection and preparation of the illustrations for these volumes were under the efficient direction of Dr. W. J. G. Land. Most of the illustrations are original, and many of them were made by Miss Anna Hamilton, an artist to whom great credit is due. Those that have been copied or adapted are appropriately credited to the original sources.

In the preparation of this edition of Volume II an attempt has been made to retain the general organization of the material, as far as possible, just as it was in the original edition. Moreover, wherever it could be done, the presentation has been unaltered; for Charles Reid Barnes, who wrote this volume, was a great master of the art of presenting material to the student. If any criticism can be made of his methods, it is mainly that the statements are too brief and concise, with too little elaboration, and not enough repetition of ideas to make mastery of the subject matter easy to the ordinary student.

The great strides made by plant physiology during the two decades since the first edition was published, have made necessary many changes, however, and in making the necessary additions we have tried not to depart from the clear, direct, and forceful style of the author of the first edition. For any shortcomings and failures in this

direction a lenient judgment should be accorded. Few of us possess anything like his skill in marshalling the facts and theories of plant physiology, and probably no one since his time has developed the splendid critical powers he possessed in this field.

In presenting the new matter pedagogical expediency has determined to a certain extent, the things which should be included, and those that should be excluded. In particular, the choice of literature for citation has frequently been determined by pedagogical considerations. For the beginning student, a paper which summarizes a situation well, even if it adds no new data, is often the most valuable source of information.

The introduction of a large literature list represents a departure from the original methods of presentation. The situation has changed since the first edition was published, and it is no longer the custom to avoid the original sources in the undergraduate work. The sooner the student becomes familiar with the research of others in plant physiology, the sooner will he be in position to accomplish something in extending the confines of our knowledge of plant behavior.

Criticism of the work in its present form is invited. No one without the helpful criticism of friends is likely to produce a work without some serious flaws. Those who may use the book should share with those who have been responsible for its revision their experiences of success or failure with it in the hands of students. Such coöperation will make it possible to develop a work which will measurably meet the needs for a simple introduction to plant physiology.

It should be recorded here that the completed manuscript of the revision of Vol. II was read by Dr. S. V. Eaton, who made a number of suggestions for its improvement.

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PLANT PHYSIOLOGY

INTRODUCTION

THE relation between the form and structure of a plant and its behavior is very intimate and to a large extent reciprocal. Form and structure in general determine behavior, and behavior, especially as it is itself controlled by external agents, to a great degree determines form and structure. It is not possible at present to discover all these reciprocal relations, much less to describe them in terms of physics and chemistry. Nor is the behavior of plants sufficiently known to be explained in these terms. Progress is being made, however, in determining these difficult reciprocal relations. The goal of physiological research, aside from the extension of human knowledge, is the ultimate control of plant production. The discovery of the carbohydrate-nitrogen balance[1] as a factor in the vegetative and fruiting behavior of various cultivated plants, and the discovery of the influence of day length,[2] and of temperature,[3] in initiating sexual maturity of many plants, are steps toward intelligent control of the growth processes of all kinds of plants.

Morphology, concerned with form and structure, is particularly interested in how each plant comes to be what it is in the short history of its own life (ontogeny), and also seeks to form a conception of how plants have come to be what they are in the long course of their history since they began to develop on the earth (phylogeny). The former topic is clearly open to experimental study and constitutes the field of experimental morphology. But the latter is much less

[1] Kraus, E. J., and Kraybill, H. R. Vegetation and reproduction with special reference to the tomato. *Oregon Agr. Coll. Exp. Sta. Bull.* No. **149**: 1–90. 1918.

Roberts, R. H. Relation of composition to growth and fruitfulness of young apple trees as affected by girdling, shading, and photo-period. *Plant Physiol.* **2**: 273–286. 1927.

[2] Garner, W. W., and Allard, H. A. Flowering and fruiting as controlled by the length of day. *U. S. Dept. Agr. Year Book 1920*: 377–400. 1921.

[3] Gilbert, B. E. Interrelation of relative day length and temperature. *Bot. Gaz.* **81**: 1–24. 1926.

open to experiment; scarcely at all, indeed, except for the determination of the laws of heredity, a field which has been called "experimental evolution." Obviously such experiments, whether in the field or laboratory, cannot be wisely planned or executed without a thorough knowledge of plant physiology.

A wide range of facts is open also to mere observation, because the ordinary changes in climate and soil, some of which are produced by other plants and animals, affect the form and structure of plants. This field is part of that distinguished from physiology proper as Ecology. Naturally even the most careful observations need to be confirmed or corrected by experiments. Thus this portion of ecology and experimental morphology are mutually related, and both really form a part of physiology in the broadest sense, and depend upon it. Physiology, in its turn, seeking to expound the phenomena of plant life in terms of matter and force, depends upon the data of chemistry and physics. In certain directions present knowledge is almost or quite sufficient to permit the framing of physical and chemical explanations. In others the data of chemistry and physics are not yet adequate for this; and in still others it seems now quite improbable that the phenomena can ever be analyzed in terms of matter and force. It must not be forgotten, however, that this is the direction of all recent advances, and that what is hopelessly obscure often becomes beautifully clear as some new vantage point widens the view.

In its broadest sense, then, plant physiology includes the study of the behavior of plants of all sorts, and of all the ways in which this is affected by external agents of every sort. On the one hand it overlaps morphology, and on the other it includes a large part of ecology. In this book, however, it is restricted in the main to a consideration of the behavior of the larger plants, especially seed plants, though in certain cases reference is made to others. In this volume no section on reproduction will be found. That topic is relegated to Morphology (Volume I), since the purely physiological processes are relatively simple, so far as known, and very much alike, whereas the reproductive organs are very different in different groups of plants and are most significant for their morphology. For convenience, also, the effect of external agents on plants is treated so as to develop and illustrate general principles, whereas a more extended account of specific cases will be found in Volume III on Ecology.

CHAPTER I — THE MATERIAL INCOME OF PLANTS

1. THE PLANT CELL

An organ. — At a glance one sees that the body of an ordinary green plant, such as a bean, is segmented, certain parts being clearly marked off by form from others. The colorless root grows in the soil; the green shoot grows in the air and consists of a distinct stem with lateral outgrowths, the leaves. Anatomically, these parts are *members;* but as the work of the plant is distributed among them, each has its *functions*, and physiologically each is an *organ*. An organ may, therefore, be defined as a part of a plant which has some definite function to perform.

A cell. — When one of the organs of the bean, such as a leaf, is inspected, one sees that it, too, is made up of parts, the petiole and the leaflets. The latter are composed of ribs and veins, with green tissue, or mesophyll, between. These parts also have certain functions and hence may be called organs. A microscopic examination of the mesophyll reveals that it is composed of minute bits of living material which is called *protoplasm*. Each individual mass of protoplasm is a *protoplast*, separated more or less completely from its neighbors by membranes or cell walls, which these protoplasts have formed. The membrane and protoplast constitute a *cell* (fig. 1).

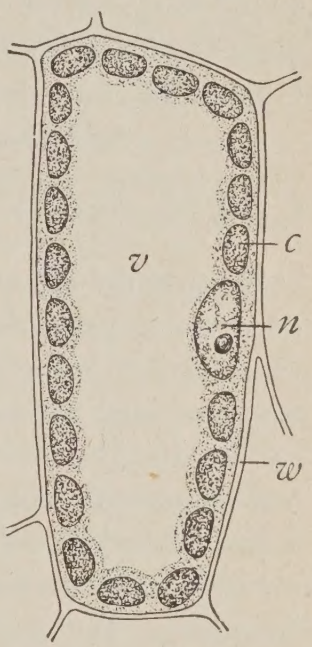

FIG. 1. — Diagram of a mesophyll cell of a leaf; *c*, chloroplast; *n*, nucleus; *v*, vacuole; *w*, cell wall.

Organs of a cell. — When the protoplast is examined more closely, a general translucent material, the cytoplasm, may be distinguished from various inclusions. There are (*a*) many very minute particles, whose nature is obscure, possibly food granules, which tend to make the cytoplasm opaque; (*b*) minute clear spaces, more fluid and sometimes watery, the vacuoles, many of which coalesce as they enlarge with age, and form a few relatively very large water spaces or only

one; (*c*) a roundish nucleus; (*d*) numerous oval green bodies, the chloroplasts; (*e*) colorless plastids known as leucoplasts, found mainly in the cells of storage organs, and serving to form starch grains within themselves; (*f*) small bodies known as chondriosomes, or mitochondria,[1] which are visible in properly stained material, and which are thought to develop into the plastids such as chloroplasts and leucoplasts. Of these, the nucleus and chloroplasts, having definite though only partly known functions, are often called organs of the cell.

The unit of function. — The word "organ," then, is applied to parts most diverse as to size and complexity; it designates merely a part when its work is thought of rather than its structure. Since the various parts of a cell do not work properly when separated, the cell may be considered as the unit of function, as it is, for convenience, known as the unit of structure. The total work of the plant is to be looked upon as simply the sum of all the work done by the individual coöperating cells.

Naturally, cells accustomed to association with others do not work properly when separated; but there are plants whose whole body is a single cell. This fact has influenced the conception of the cell as a unit.

Work of the cell. — The work which any plant or part of a plant can do depends primarily upon the working equipment of the cells, and the ultimate form and structure of the mature cells. Thus, a cell well provided with chloroplasts will be a food manufacturing cell if carbon dioxide, water, and sunlight energy are available, as occurs in leaf mesophyll. Or if the cell has numerous leucoplasts, it is usually a starch storage cell. If it has large vacuoles and thin protoplasmic membranes, it may function in the intake or transfer of water through the plant. If the cells are elongated, they frequently serve for conduction of water and soluble organic foods. If they are heavy walled, they serve for mechanical support and protection. Embryonic cells, with large and rapidly dividing nuclei, function in the growth of cambium, or stem and root tips, and in the formation of new organs. If chromoplasts (bodies colored other than green) are present, the cells may form some of the brightly colored portions of flowers and fruits. In general it is obvious that the function which any portion of the

[1] Guilliermond, M. A. Sur l'origine mitochondriale des plastides. *Compt. Rendu. Acad. Sci.* Paris **167** : 430–433. 1918.

Mottier, D. M. Chondriosomes and the primordia of chloroplasts and leucoplasts. *Ann. Bot.* **32** : 91–114. 1918.

plant can perform depends upon the cellular equipment, the organs present within the cells themselves.

The cell wall. — Each protoplast jackets itself with a membrane, which usually shuts it off completely from the outer world and from its neighbors, except for some exceedingly minute threads of cytoplasm, known as plasmodesmen, by which it remains connected with them. These threads, traversing the cell wall, persist from the time of its formation. The protoplasts are much hampered by these walls in certain ways, though compensating advantages doubtless accrue. For instance, the movement of the protoplast is restricted, and it cannot engulf food particles, but is limited to the substances which can dissolve in water and so migrate through the wall. Thus the cell wall becomes a factor of prime importance to the plant.

The cell wall is the most easily observed and striking part of the cell; in fact the word itself commemorates the discovery of the empty chambers of cork and charred wood which Hooke and Malpighi and Grew saw (1667–1671) with their primitive microscopes, and thought the fundamental feature of plant structure.

Removal and alteration of the wall. — The cell wall, formed by the protoplast, is subject to partial or complete removal by it. In green plants it is usually composed at first of a pectic middle lamella, upon which cellulose layers are deposited. With increasing age it is subject to various modifications, which alter its relation to water and thus profoundly affect the conditions of life of the protoplast within.

One alteration to which the wall is subject is known as cutinization, because cutin, a waxy substance, is deposited or formed within it. Sometimes, as on the outer face of superficial cells, this takes place to such an extent as to form the cuticle, a layer which may be loosened and removed entire from the rest of the wall. Parts of the outer wall adjacent to the cuticle may also become impregnated with cutin to varying degrees. The cuticle and these cutinized layers repel water, so that a minimum only is found in the wall and little can pass through. The leaves of plants are generally cutinized, and the cutin itself is a condensation product of cutinogenic acids.[1] This condensation is favored by the partial drying of the leaf surfaces, where the waxy anhydrides of the acids are deposited.

[1] Priestley, J. H. Suberin and cutin. *New Phytologist*, **20**: 17–29. 1921.
Lee, Beatrice, and Priestley, J. H. The plant cuticle. Its structure, distribution, and function. *Ann. Bot.* **38**: 525–545. 1924.

Similarly, the cells of plants may become suberized, as in the peeling of the potato. In this case it is suberogenic acids which have been condensed into the complex anhydrides which we call cork or suberin.

By another modification portions of the wall may become gelatinous. When wetted, they take up great quantities of water (sometimes as much as 98 per cent of their wet weight) and swell so enormously as to lose altogether their usual firmness.

Again, the wall may become lignified, a condition characteristic of the walls of woody tissues, whence the name. Lignified walls do not swell so remarkably as gelatinized ones, but they allow water to pass through them with comparatively little resistance.

Water of the plant. — From what has been said it is evident that water forms an important part of the cell; but it is necessary to comprehend its intimate relations to every part in order to understand its full significance. In ordinary land plants water constitutes always over one half and usually about three fourths of their weight. Of the least watery parts, such as wood, it forms one half, and of the most watery parts, such as the pulp of juicy fruits, as much as 95 per cent. In ordinary speech it is common to indicate the general character of an object by naming its most abundant component; as, a wooden table, a brick wall, wood and brick being respectively the dominant but not the only material in the structure. If the water of the plant were visible to the eye, distinct from the other constituent materials, on the same principle a plant might be spoken of justly as water, held in form by other substances mingled with it. This is quite the reverse of the ordinary conception, but its essential truth becomes evident when we consider not merely the quantity of water relative to other constituents, but attempt to picture the relations of water to the various parts of the cell.

Imbibition. — When a plant is placed in dry air, water evaporates from it and its various parts shrink and shrivel. A little shrinkage occurs when plants wilt on a hot, dry day. When water again enters in sufficient quantity, they swell and regain their fresh look. The water may even be driven out entirely from some plants, as certain mosses, and when again wetted, the parts swell and regain partly or wholly their original dimensions. The most obvious of these changes are due to the collapse or expansion of the cells; but that they are not limited to alterations in the dimensions of the cells may be shown by measuring a dry bit of cell wall or a dry starch grain under the

microscope, and after wetting, remeasuring it. On examination it appears that almost every substance in the plant body is capable of imbibing water, and of swelling or shrinking as the proportion of imbibed water increases or diminishes. This property by virtue of which dry organic matter will take in water and swell as it becomes wet is called *imbibition.*

That imbibition occurs with considerable force is illustrated by the fact that stone was formerly quarried by driving dry wood into holes drilled in the rock, and then wetting the wooden pegs. Recent measurements indicate that air-dry matter, such as dry seeds, will take in water with an initial force of almost 1000 atmospheres.[1] As the dry substance becomes moist, its power to take in any more water diminishes, until at the point of saturation this imbibition force reaches zero.

Even air-dry matter still contains some imbibed water, which can be removed only by prolonged heating. This hygroscopic water, as it is called, is held by forces which are greater than the forces causing evaporation. In the case of oven-dried starch it has been estimated that the starch imbibes water with a force of more than 11,000 atmospheres.

The smaller the quantity of water present in any substance the more difficult it is to remove it, and the larger the amount present the more readily it can be removed. From the fully swollen gelatinous body of a sea weed, *Laminaria*, some water may be extracted by the pressure of the fingers, while the greatest pressure possible does not suffice to squeeze it all out.

Imbibition performs several useful functions in plant life. It causes the intake of moisture by seeds when planted, and thus provides the essential condition for speeding up respiration and the renewal of growth. It also maintains the more or less nearly saturated condition of cell walls and protoplasm in the living plant, and through the imbibition forces developed when saturation deficit occurs in the aerial shoot it helps to transport water through the plant body. These forces will be referred to again in connection with transpiration and the ascent of sap in plants.[2]

[1] Shull, C. A. Semipermeability of seed coats. *Bot. Gaz.* **56**: 169–199. 1913. (See pp. 184–190.)

[2] ——. Imbibition in relation to absorption and transportation of water in plants. *Ecology* **5**: 230–240. 1924.

Theoretical structures of organized bodies. — In order to understand the significance of imbibitional swelling, it is necessary to consider the ultimate structure of the organic materials which make up the plant body. It is now generally recognized that nearly all of the more or less solid parts of the plant body are in the colloidal state. This means that the cell walls, protoplasm,[1] and protoplasmic inclusions are in such a fine state of subdivision that the individual particles would be invisible even with the highest power microscopes, but not so small as chemical molecules. The particles are said to be ultramicroscopic, and are from about 0.00003 to 0.00014 millimeter in diameter. Each particle is an aggregate of molecules, and these colloidal particles are called *micellae.*

In swelling, the water may not only surround these micellae, forming films which tend to separate the particles from one another, but it may also penetrate them in such a way that the water may be thought of as dissolved in the colloidal particles of protoplasm and cell wall. The colloidal substances whose micellae can hold large amounts of water, either on their surfaces or within them, are said to be hydrophile colloids. Much of the plant body is made up of hydrophile colloidal material, and the shrinkage on drying, and the swelling during imbibition, should be easily understood from this point of view. As water enters the tissues, the micellae tend to separate, and increase in size from the bound water. On the other hand, a diminution of water causes the particles to approach one another more closely, and to shrink in size as the colloidally held water evaporates from the micellae.

The separation of the micellae is limited by the forces of cohesion acting between them. In dry matter the forces causing swelling are at first greater than the cohesion forces in the presence of water, and the particles separate. But as separation occurs, the cohesion forces increase; at the same time the forces of imbibition decrease with water intake. When these two sets of forces are balanced in the presence of water, the substance is saturated. There is no more tendency to take in water, and no tendency for further separation of the colloidal micellae. The micellae of the swollen material usually remain so related to one another that when the water is all removed, the material resumes the same form that it had before swelling occurred. However, this is not always the case.

[1] Lepeschkin, W. *Kolloidchemie des Protoplasmas.* Springer. Berlin. 1924.

Swelling and solution. — In the recovery of the original form is a practical but only a partial difference between the behavior of merely swollen and of dissolved substances. In both swelling and solution water wanders in among the particles and separates them more or less widely. But there comes a limit to the swelling, and no more water enters. If it is removed, the body regains its form and the particles, presumably, their identical position. In solution there is no limit to separation, except by the amount of water present; and when it is removed, the particles rearrange themselves in forms which may be similar to those of the original body, but are obviously not identical with them. Yet swelling may become excessive, as when starch grains are put into hot water or alkalies, and after certain limits are passed the swollen grain will not regain its normal form. By such transitions imbibition merges almost insensibly into solution.

Relations of inner and outer water. — For further understanding it is useful to attempt to picture the relations of the water to the other components of a young cell immersed in natural water. The outside water has particles of many sorts scattered through it; for no matter how pure, in nature all water is really a dilute solution of various substances. The water of the cell wall has so many particles of cell-wall stuff scattered through it that nearly half the volume is cellulose; but it is continuous with the water outside. The water of the cytoplasm and of its inclusions is freer of these substances, *i.e.* it is more nearly pure, because the cytoplasmic particles form only about one fifth of the whole mass. This water, too, is continuous with the water of the cell wall, and with that of the solution outside. The water of the vacuole is still less encumbered with other particles, only one or two per cent, perhaps, but these are of diverse kinds, for the cell sap is a solution of many things. The water here is likewise continuous with that outside through the cytoplasm and wall (fig. 2).

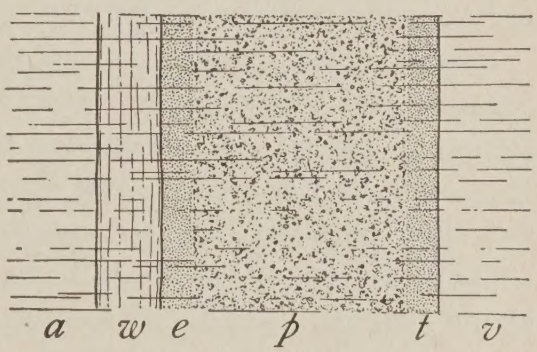

FIG. 2. — Diagram of an imaginary section through the cell wall and protoplast to show the possible relations of water to the cell; *a*, outer water; *w*, cell wall; *e*, ectoplast; *p*, general cytoplasm; *t*, tonoplast; *v*, vacuole (inner water); *e*, *p*, *t*, belong to the protoplast. The water in this way forms a continuous pathway for entry of dissolved substances into the cell.

Continuity of water. — The diagram on page 9 may be applied to any plant cell by modifying it to fit special features, and may furnish a working hypothesis, crude though it be, of the invisible structure of organic bodies in general. This hypothesis is conceived to co-ordinate the observed facts of structure and of the migration of substances into the plant. The continuous cell wall excludes the intake of solids, and determines that only substances soluble in water can enter the body. But according to this picture a continuous waterway is provided along which water-soluble substances may travel. Now in order to conceive how this migration occurs, one must have a mental picture of the behavior of watery solutions. To get such a picture it is necessary to bring to mind certain ideas of physicists regarding matter in its various states.

2. DIFFUSION AND OSMOSIS

For convenience, matter is said to exist in three states: gaseous, liquid, and solid. The state in which any particular substance is found in nature depends very largely on the amount of molecular attraction which exists between the molecules of that substance at ordinary atmospheric temperatures and pressures.

Gases. — One characteristic of gases is that their particles tend to separate and to occupy to its utmost limits any receptacle in which the gas is placed. If unconfined by impermeable walls on one side, they form no free surface, but show unlimited capacity for diffusion, and their particles may become so dispersed among the other gases constituting our atmosphere as to be unrecognizable by any means at our disposal. This distribution of the particles is independent of any mixing by mass movements, such as those which show as air currents or arise by jarring or stirring. On the contrary, it is assumed to be due to the kinetic energy of the gas molecules themselves, being hastened by any means which imparts energy, as by the application of heat.

Liquids. — The molecules of liquids are much less mobile than those of gases. When placed in a container, they shape themselves to it and form a free surface that is horizontal under the action of gravity, from which particles may fly off as vapor into the air. In volatile liquids this vaporization takes place at ordinary temperatures to such an extent that the process is easily measurable; in others, called non-volatile, the movement is too slight to be observed, or is

masked by other changes. Increasing the molecular energy of the liquid, as by heating it (unless it dissociates too rapidly), hastens its conversion into vapor, which behaves nearly or quite as a gas.

Solids. — The particles of solids are still less mobile than those of liquids, so that solids retain more or less perfectly their own shape, except under stress. Some solids, like ice and iron, can be liquefied and then vaporized; others, like camphor, may vaporize without passing through the liquid state. In the latter case the substance is said to sublime.

Solution. — In every state of matter there exists a tendency of the molecules to separate, hampered more or less by their cohesion or mutual attraction. Even very dense solids, such as lead and gold, when placed in contact, show intermingling along the line of contact, though this is so slow as to be actually measurable only after a long time.[1] But when certain solids and liquids are brought together, the intermingling occurs so speedily as to attract attention, and the solid is said to dissolve in the liquid. The liquid then is known as the *solvent*, and the former solid as the *solute*.

When a crystal of some substance, as copper sulphate, dissolves in a solvent such as water, the surface molecules of the crystal are being continually loosened from their positions, and migrate away from the crystal into the surrounding water. The water molecules are largely responsible for this loosening effect on the copper sulphate molecules, for, although the latter are in a state of kinetic vibration which tends to separate them, the water molecules are more active, and tend to penetrate the crystal. The water molecules are also in kinetic motion, and by their impacts against the salt molecules tend to jar these out of their positions in the crystal surface. At the same time the physical and chemical attractions existing between the copper sulphate and water molecules are so great that they overcome the chemical attractions of the crystal molecules or ions for each other. The result of all these complex forces is that the copper sulphate dissolves and travels slowly through the water toward regions where there are fewer copper sulphate molecules.

The rate at which a crystalline or mineral substance dissolves in water depends partly upon the ease with which water overcomes the

[1] In an experiment in which a rod of lead and a disk of gold were kept in contact for four years, the gold had diffused over 7 millimeters from the contact surface, in amounts appreciable by assaying.

forces of cohesion of the crystal. If the cohesion attractions are small, the substance dissolves readily. If they are relatively large, the substance dissolves more slowly. When the solubility is very low we speak of insoluble substances; but even glass reagent bottles give off molecules slowly into the water stored in them, and the most resistant soil minerals slowly dissolve in the water of the soil.

Gases also dissolve in liquids. In like manner when two liquids can be mixed (*i.e.* are *miscible*), their particles become intermingled; then one may be considered as the solvent and the other as the solute; *e.g.* glycerin and water. All gases are miscible and in all proportions; but not all liquids (*e.g.* oil and water), nor all solids and liquids. Otherwise stated, when one substance dissolves another, the two do not always mix in all proportions; usually there is a limit to the ratio of solvent to solute, and when the limit of intermingling is reached (a condition called saturation), any excess of the solute remains undissolved. Saturation is readily explained. As soon as a crystal or mineral substance begins to dissolve in water, there is a tendency for some of the dissolved solute molecules to return into the crystal. During the early stages of solution, when only a few molecules are dissolved from the crystal, many more molecules are being loosened and leave the solid than enter it. But as the solution becomes more concentrated with dissolved solute molecules, the number returning to the crystal in unit time constantly increases, while the number loosened in the same time decreases. Finally the numbers of molecules leaving the crystal and entering it in a given time become equal, and this is the state of equilibrium existing between solution and crystal at saturation.

Nature of solution. — It is not necessary to the idea of a solution that the mixture should be liquid, though this is the popular usage. A solid, a liquid, or a gas may " dissolve " in a solid and the solution be a solid. Glass is considered a solid solution. Again, a gas may " dissolve " in a gas and the solution be gaseous. For our purposes, then, a solution is a mixture of substances so intimate that they cannot be mechanically separated; as, for example, by filtration.

The actual chemical state of the substances is not completely known. The solute always exists partly, and sometimes wholly, in the molecular state of subdivision. But many solutes undergo dissociation in water, forming electrically charged bodies called ions. Thus sodium chloride forms sodium ions positively charged, and chlorine ions negatively charged, in addition to uncharged sodium.

chloride molecules. Substances which thus dissociate, or ionize, can conduct electric currents and are therefore called electrolytes. Other substances such as the sugars which do not ionize are called non-electrolytes.

The relation of the molecules and ions of the solute to those of the solvent are also complex. Water at low temperatures is not merely H_2O, but has molecules made up of two or three H_2O groups joined together. In solution, the molecules and ions of the solute probably unite in part chemically with the water to form hydration complexes. The actual structure of these complex hydration compounds is not known. Although solution is so intimate a mixture that mechanical separation of solvent and solute is not ordinarily possible, yet by mingling finely divided but insoluble substances, such as lamp black, with a solution, many particles of the solute may be taken out by adsorption, so that this sort of partial mechanico-chemical separation is possible.

Water as a solvent. — Almost the only liquid which is of much significance in plant life as a solvent is water,[1] and this is capable of dissolving more different substances than any other known; whence it is said to be the most general solvent in nature. In water solutions the particles of the solute behave as those of a gas; they may diffuse to the limits of the solvent, for its boundary forms the only limit to their movements.

Natural solutes. — Water is widely distributed in nature, and comes in contact with many things; first, as it falls in a spray through the atmosphere, and then as it percolates through the soil and rocks or flows over their surface. Hence, natural waters hold many solutes, and are almost always in position to acquire more if any of the dissolved molecules are removed by chemical action. Thus, the water in arable soils contains everywhere much the same amounts and kinds of mineral salts;[2] for, though soils differ greatly in the proportion of their constituents, the quantities of mineral solutes are kept nearly constant by the steady dissociation of the dissolved minerals, by the further solution of any substance which has disappeared from the water for any reason, and by the movement of solutes from one point to another.

Diffusion. — If solutes are free to diffuse through the water to its utmost limits, what determines the direction and rate of this movement? Imagine a crystal of a soluble salt placed in a tumbler of water (fig. 3). The particles fly off from the surface of the crystal and become numerous in the water immediately adjacent. Here, freed partly from the mutual constraint of the crystalline condition, they may be con-

[1] Steel, Matthew. *Physical Chemistry and Biophysics.* chap. vi. Water, the greatest solvent. John Wiley & Sons, Inc., 1928.

[2] Cameron, Frank K., *The Soil Solution,* Chemical Pub. Co. 1911.

ceived to be in rapid movement to and fro, colliding often with their fellows where these are most numerous and less often where they are fewer. Hence, in regions towards the crystal, rebuffs are most frequent; consequently the particles are continually working out into parts of the solvent more and more remote from the crystal and the crowd of salt particles, the final result being an equal distribution throughout the solvent. The movement is from the region where the particles are most numerous to that where they are less numerous, *i.e.* from the regions of higher *concentration* of the solute to regions of lower. Or, since gas pressure is conceived to be due to the impact of the molecules on the sides of the container, and since the solute behaves as a gas, it is from regions of higher to regions of lower *pressure*. For convenience, the tendency of solutes to diffuse may be called diffusion pressure or diffusion tension.

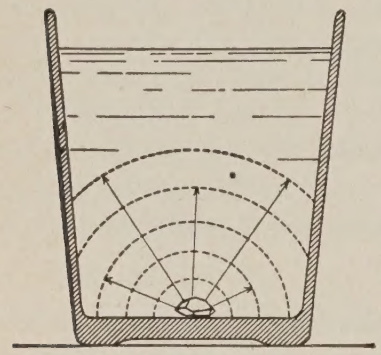

FIG. 3. — Imaginary section of a tumbler of water with a soluble crystal, showing by arrows the direction of diffusion, and by dotted circles the lines of equal concentration.

Rate of diffusion. — The rate of movement of diffusing particles of any solute depends on the *difference* in concentration, or the *gradient* of the pressure. Thus, when a very soluble crystal is put into a solvent, the rate of diffusion is at first rapid, because a very high concentration of solution is adjoined by a zero concentration; the gradient is " steep " because the solute at very great pressure adjoins the pure solvent of zero pressure. But the rate constantly falls as diffusion progresses, since the difference at any two points is becoming less and less. The rate is also greatly influenced by temperature, an increase accelerating and a decrease retarding the rate, exactly as in gases.[1]

Osmosis. — Returning now to the conception of the relation of water to the plant cell: it was seen that water is continuous from the soil through the walls and protoplasm and vacuoles of cells throughout the plant body. This water is important not only in providing the conditions necessary to activity on the part of the protoplast, but it forms a continuous pathway everywhere for the diffusion of such solute molecules as may be needed by the living cells, and which

[1] To avoid misunderstanding it may be necessary to add that under like conditions each solute diffuses at a rate peculiar to itself.

have to migrate through the various membranes and vacuoles to reach the place of ultimate use.

It might seem, with waterways for diffusion in any direction, that any solute, inside the plant or outside of it in the soil or surrounding water, might diffuse in any direction in which its concentration is lower. But sometimes solutes are not allowed to diffuse in directions where the concentrations are lower because the membranes, cell walls, and protoplasmic membranes, may interfere with the free diffusion or modify the rate of diffusion of certain particular solutes.

It must be remembered also, that water is not static in the plant. It too can move from place to place by diffusion, and in its diffusion water obeys the same laws as solutes. The water tends to diffuse from places where water molecules are abundant and close together, to regions where they are fewer and farther apart. In other words, water too travels from places of high concentration of water toward places of low concentration of water, just as a salt diffuses from a place of high concentration to places of low concentration of that particular salt. The diffusion of water through the cell walls and protoplasmic membranes occurs usually with more freedom than the diffusion of solutes, but we have already seen that modification of the wall membranes, as by cutin or suberin (cork) modifies the rate of passage of water through membranes; so that water moves through the living cells of the plant in accordance with the same laws of diffusion that express the behavior of the solutes in their migration from place to place.

Now, diffusion through membranes or partitions, particularly differential diffusion, is called *osmosis*. While some authors have confined the term osmosis to diffusion of water through more or less semipermeable membranes, we have just seen that water diffusion is not different in principle from salt diffusion. So we may speak of the osmosis of solutes, as well as the osmosis of water. However, since we are accustomed to call solute osmosis simply diffusion, and water migration through membranes osmosis, the term osmosis is used here to mean water osmosis. As thus used, we may define osmosis as *the diffusion of water through a membrane in response to an unequal distribution of water molecules on opposite sides of the membrane.* The diffusion occurs in that direction which tends to produce equalized distribution of water molecules on opposite sides of the membrane.

Osmotic pressure. — If water diffuses through the protoplasmic membranes into a cell more rapidly than it is leaving that same cell, the volume of the vacuole is increased, and the water exerts a pressure upon the walls of the cell, sufficient to cause the cell walls to stretch. The cell in this condition is said to be *turgid*, or swollen, with the contained liquid. If one takes a large turgid cell of *Nitella*, and punctures it with a needle, the water may be seen to spurt from the cell, showing that there is a real pressure of liquid inside the cell. This pressure is called *osmotic pressure* because it is produced by osmosis. Formerly it was thought that this pressure was caused by solute molecules in the vacuoles, acting like a gas to cause pressure upon the protoplasmic wall which resisted their passage. There were reasons favorable to such an interpretation, but we now know that the pressure is only proportional to the amount of solutes present, but not caused by them, except as they tend to interfere with the water leaving the cell, once it has entered. A more sensible explanation of osmotic pressure is that it is caused by the water diffusing into the cell faster than it leaves it. This water diffusion is also proportional to the solute concentration in the cell sap. A homely illustration of the condition within a turgid cell is to liken it to a street car during the rush hours when more people are constantly boarding the car than leaving it per unit of time. A pressure soon exists throughout the car, only the car does not have yielding, elastic walls, and does not stretch, as the cell does.

Osmotic action and osmotic pressure is usually demonstrated by use of a thistle tube covered by a bladder membrane, and with the bulb filled with syrup. The bulb is then set into a vessel of pure water. The water now passes through the membrane by osmosis, and increases the volume of the syrup, which rises in the stem of the thistle tube. As soon as the liquid rises above the level of the water in which the thistle tube has been placed, a hydrostatic pressure develops, equal to the height to which the column has risen, about 15 pounds to the square inch for a 32 foot rise.

The actual osmotic pressure here is the pressure of the water molecules passing through the bladder membrane in response to the unequal distribution of water on opposite sides of the membrane, for the syrup has fewer molecules of water per unit volume than the pure water surrounding the thistle tube.

But as soon as hydrostatic pressure begins to develop by rise of

the liquid in the tube, this hydrostatic pressure begins to cause more of the water molecules to diffuse back from the syrup into the water. As long as more molecules of water pass from water to syrup than from syrup to water, the column continues to rise, but the increasing hydrostatic pressure is constantly reducing the difference between inflow and outflow of water. Theoretically, the liquid should rise in the thistle tube until the hydrostatic pressure of the column is just equal to the osmotic pressure of the inflowing molecules. At this point the number of molecules of water diffusing through the membrane in opposite directions should be equal, and the column should become stationary. When this point is reached, although there is still unequal distribution of water on opposite sides of the membrane, yet the water has reached dynamic equilibrium, with the whole system under pressure equal to the osmotic pressure of the diffusing water.

As a matter of fact we never secure the theoretical result with thistle tube experiments because our membrane is imperfect. It stretches under the hydrostatic pressure, or leaks, or is injured by bacterial action; and after the column of liquid rises 8 or 10 feet, it may fall. Moreover, the sugar molecules of the syrup slowly diffuse through the membrane into the surrounding water, and tend to reduce the water concentration on the lower side of the membrane, and thereby to reduce the osmotic pressure.

Membranes have been made, however, by chemical means, which are almost perfect. Thus Pfeffer about 1877 used copper ferrocyanide membranes, precipitated in porous clay cups, with which he performed his famous experiments on osmotic pressure, which were used about ten years later by Van't Hoff in developing the theory of solutions. Still more recently Morse and Frazer at Johns Hopkins University used copper ferrocyanide membranes in making the most accurate quantitative measurements of osmotic pressure ever made.

Measurement of osmotic pressure. — It becomes necessary at times to determine the osmotic concentration of the cell sap of plants. Thus one may need to know the influence of some given climatic factor, or of climate as a whole upon the concentration of the tissue fluids of plants. The accepted research method is to determine the freezing point of the tissue fluids, either by electrical means, or by use of the Beckmann thermometer. A solution always has a lower freezing point than pure water, and by experiment it has been found

that a solution of sugar containing a gram molecular weight of sugar per liter of water depresses the freezing point of the solution so that it freezes at − 1.85° C. instead of at 0° C. By other experiments it has been shown that if such a solution were inclosed in a cell into which water could enter by osmosis while the sugar could not pass in the opposite direction, the osmotic pressure would be about 22.4 atmospheres. Therefore, a depression of − 1.85° C. in freezing point is considered to indicate an osmotic concentration equal to 22.4 atmospheres. Tables have been prepared by which one can readily read off the osmotic pressure from known freezing point depressions.[1]

Another method, less accurate, but frequently used in early investigations of osmotic pressure, is based on what is called plasmolysis, or the withdrawal of the protoplasm from the cell wall by use of solutions of known concentration. The plasmolytic method is convenient, but serves only for rough determinations. The nature and significance of this process will be considered later.

Permeable and impermeable membranes. — It has been noted that the character of the plant membranes may modify the rate of diffusion of water, salt molecules, or ions, into the plant or from place to place in its body. The properties of these membranes must now receive careful consideration. Some membranes allow not only water, but all kinds of salts in solution to pass readily through them. Both water and solutes dissolve in and diffuse through these membranes. A membrane of this type is called a permeable membrane. If on the contrary neither water nor dissolved substances will pass through the membrane, it is said to be impermeable. In still other membranes water may dissolve in and penetrate the membrane, while some particular solute dissolved in the water may not be able to dissolve in

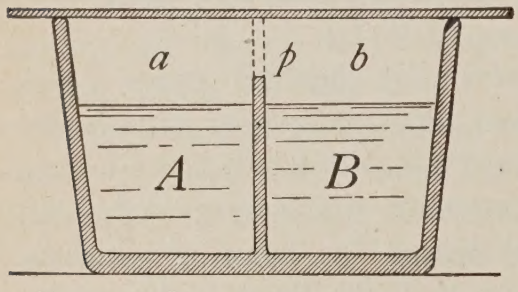

FIG. 4. — Diagram: *A*, pure water; *B*, watery solution of salt, or sulphuric acid; *p*, portion of the partition supposed to be removable; *a*, *b*, air.

[1] Harris, J. A., and Gortner, R. A. Notes on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing point, with a table for the values of *P* for △ = 0.001 to △ = 2.999°. *Amer. Jour. Bot.* **1**: 75–78. 1914.

Harris, J. A. An extension to 5.99° of tables to determine the osmotic pressure of expressed vegetable saps from the depression of the freezing point. *Amer. Jour. Bot.* **2**: 418–419. 1915.

the membrane at all. The water may pass, but the solute not. Such a membrane is described as semipermeable. A simple physical apparatus will be considered first. Suppose in a closed glass vessel (fig. 4) a glass partition divide *A*, pure water, from *B*, a watery solution of salt. No interchange of water or salt between *A* and *B* is possible through such a partition, whence it is said to be impermeable. But if the partition be made of some substance with whose particles salt particles can mingle — a substance, that is, with which salt forms a solid or semi-solid solution — then the salt particles which by diffusion reach the *A* side of the partition may fly off thence into the water, *A* ; and they will do so, provided the attraction of the water for the salt is greater than that of the partition stuff for the salt or provided that the size relations and electric charges of the pores [1] of the membrane to the hydrated ions in *B* are such as to permit passage. The nature of the partition, then, determines whether any substance may pass through it, and of course modifies the rate of its diffusion.

This is well illustrated by using air as the partition. In fig. 4, suppose *A* to be pure water and *B* sulphuric acid, with the impermeable glass partition reaching only a little beyond the top of the two liquids, the space above them being filled with air. Water (as vapor) can mingle with air, *a*; sulphuric acid does not vaporize measurably; *i.e.* the air, *b*, is practically impermeable to it but permeable to water. Water particles therefore reach the *b* surface of the air partition and enter the sulphuric acid. Hence the water level in *A* falls; the acid level in *B* rises.

Or, again: if one place carefully in a tumbler (fig. 5) chloroform, *c*, water, *w*, and ether, *e*, the water may be considered as the partition. Ether, being freely soluble in water, diffuses into it and reaches the surface of *c*. Being also soluble in chloroform, it moves on from this surface, diffusing in the chloroform. The chloroform, being only slightly soluble in water, diffuses into it but slightly. Finally, there remain only two mixtures: the water saturated with ether and chloroform, and the chloroform saturated with water and containing the rest of the ether. This experiment illustrates not only the solvent action of the partition, but also the way in which the relations of solubility between the partition and the liquids that it separates determine the dominant direction of diffusion.

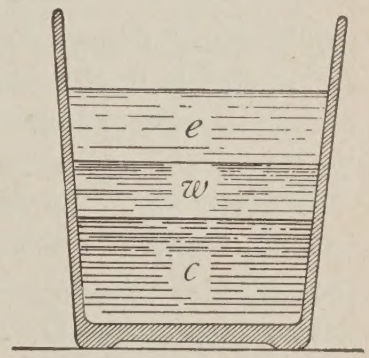

FIG. 5. — Diagram: *c*, chloroform; *w*, water; *e*, ether.

The cell wall membrane. — Among the plant membranes through which solutes pass, the cell wall has been thought to exercise little

[1] Bartell, F. E. Membrane potentials and their relation to anomalous osmose. *Colloid symposium monograph* 1 : 120–135. 1923.

selective influence. It is usually permeable to most if not all substances presented to it in nature. Nevertheless, the non-living testae of seeds, made up mainly of cell walls modified by waxy or lipoid substances, are frequently impermeable to water, or to particular solutes, either gaseous or mineral. Thus the coats of the seeds of honey locust, *Canna*, various Malvaceae, and some common legumes like clover and alfalfa, are frequently impervious to water. Such seeds are known as hard seeds because they do not swell when placed in water. They are often long delayed [1] in germination merely because water cannot enter until the coat has sufficiently weathered. While such delayed germination may give a species the advantage of a time distribution, the hard seeds of clover and alfalfa grown in arid regions form a large economic problem.

Even when the seed coat is permeable to water, certain solutes may not be able to pass through these non-living membranes. The coats of *Xanthium* seeds are not penetrated by sodium chloride, nor by sugar, although they are easily permeable to water. This property in the case of water plants whose seeds lie buried under the water for long periods of time without germination, may be important in the retention within the seed of necessary solutes.

The upper seed of *Xanthium* has a coat so impervious to dissolved oxygen that it is delayed in germination [2] because the embryo plant cannot secure enough oxygen, though every other condition is provided. It is possible in this case that the seed coat also tends to retain the carbon dioxide of respiration within the seed, and to induce dormancy by this slow oxygen-carbon dioxide exchange.[3]

It is not only seed coats which have been found to act selectively; the cell walls of the endodermis [4] in the root region have selective permeability, allowing certain solutes to enter and others not.

It should be remembered, however, that the plant needs many mineral salts in its growth, chiefly the nitrates, sulphates, phosphates, and silicates of such bases as calcium, potassium, magnesium, iron,

[1] Crocker, W. Mechanics of dormancy in seeds. *Amer. Jour. Bot.* **3** : 99–120. 1916.

[2] ——. Rôle of seed coats in delayed germination. *Bot. Gaz.* **42** : 265–291. 1906.

Shull, C. A. The oxygen minimum and the germination of *Xanthium* seeds. *Bot. Gaz.* **52** : 453–477. 1911.

[3] Kidd, Franklin. The controlling influence of carbon dioxide in the maturation, dormancy and germination of seeds. *Proc. Roy. Soc. Lond.* B. **87** : 408–421, and 609–625. 1914.

[4] De Lavison, Juan de Rufz. Du mode de pénétration de quelques sels dans la plante vivante. Rôle de l'endodermis. *Rev. Gen. Bot.* **22** : 225–241. 1910.

manganese, and aluminium. Such needed minerals must be thought of as finding ready access to the living protoplasts, either as molecules or ions, as rapidly as needed. Cell walls and protoplasmic walls must be permeable to these needed salts nearly everywhere throughout the entire plant body. Any idea that cell walls or plasmatic membranes are semipermeable to these nutritional mineral elements is untenable.

Cytoplasmic membranes. — The protoplast behaves somewhat differently from the cell wall. It is obvious from microscopic examination that it is not uniform in structure. There is always next to the cell wall a delicate cytoplasmic layer, the ectoplast, and each vacuole is bordered by a similar layer, a tonoplast (fig. 2).

Since a layer, apparently of the same sort, is formed at the surface of a fragment of protoplasm released by violence from the cell wall, it seems probable that these layers are the result of a change wrought in the physical structure of the cytoplasm by contact with solutions of a certain sort, rather than that they are permanent organs, as they were once held to be. According to a physical principle known as the Gibbs-Thompson principle any substance which tends to lower the surface tension of a liquid tends to accumulate in the surface of the liquid. Protoplasm is probably a mixture of proteins, lipoids, or fat-like substances such as sterenes and sterols, soaps, pentosans, etc., of which the soaps and lipoids particularly decrease surface tension. There is reason for believing, then, that the ectoplast and tonoplast are made up of complex lipin-soap mixtures, with calcium soap and the sterols at least partially responsible for the semipermeability of these plasmatic membranes. It has been recently suggested that the sterenes may have a part in the selective semipermeability of the membranes.[1] These membranes are perhaps advantageous in protecting the cytoplasm from further change.

However formed, they are limiting membranes not only in the sense of bounding the protoplast, but also in the sense of admitting and emitting some only of the great variety of solutes that come into contact with them. Yet the share of the rest of the protoplast in this discrimination is not to be overlooked; and since it is impossible to analyze the action of each part, we may for convenience consider the protoplast as *a* membrane between the vacuole and the outer world. But for substances in the protoplast itself the ectoplast may act alone.

Selective action. — The chemical composition of the cytoplasm being almost wholly unknown and doubtless variable, no clear statement

[1] Kahlenberg, L. On the separation of crystalloids from one another by dialysis. *Philosophical Mag.* (7th series) 1 : 385–394. 1926.

can be made as to the mode of its discriminative action. It is known only that it allows many substances to pass through readily and debars others; and further, that some substances, which are usually denied passage, are permitted to pass under other conditions. Thus illumination, or changes in light intensity, or changes in temperature, oxygen supply, salts, electric currents, ageing, or anesthetics may render the protoplasm either more permeable [1] or less permeable than before. It must not be forgotten that protoplasm is in the colloidal state, and that changes in the degree of dispersion are readily produced. Such changes no doubt affect the permeability of the protoplasm. These relations are best explained by the theory that solubility in the membranes is prerequisite to osmosis. If so, a change in composition of the cytoplasm might account for the change in permeability that is observed on occasion.

It is quite possible that local differences in the composition of the cytoplasmic membranes (a sort of mosaic composition) may permit the passage of different substances at different places. There is little support for such a theory, however.

Variable selection. — The welfare of the organism is largely dependent on the discriminative action of the cytoplasmic membranes, for substances requisite to food-making are allowed to enter; and foods are not permitted to diffuse out and be lost. Chemical transformations of the most varied kind occur within the plant, both among the substances that enter it and are elaborated into foods, and also among the foods that are assimilated. Of course each change in chemical nature changes the relations of the substance to the protoplast and may modify thereby its diffusibility through it. Moreover, without known chemical change, the mere presence of one solute may greatly modify the behavior of another, either by changing the membranes, or by its direct influence upon the other solute. With membranes capable of change, and solutes capable of change, and the almost unknown extent of the influence of one solute on another, the complexity of the phenomena of osmosis has almost baffled investigation

[1] Tröndle, A. Der Einfluss des Lichtes auf die Permeabilität der Plasmahaut. *Jahrb. wiss. Bot.* **48** : 171–282. 1910.

Banus, M. G. Effect of electrical currents upon the permeability of plant cells. *Archiv. ges. Physiol.* **202** : 184–193. 1924.

Osterhout, W. J. V. Exosmosis in relation to injury and permeability. *Jour. Gen. Physiol.* **5** : 709–725. 1923.

Szücs, J. Über einige characteristische Wirkungen des Aluminium-ions auf das Protoplasma. *Jahrb. wiss. Bot.* **52** : 269–332. 1913.

hitherto, but some hopeful progress has been made recently in the discovery of factors determining the permeability of protoplasm.

It cannot be too strongly emphasized that the "selection" above described has in it no element of choice, nor does it depend upon the "needs" of the plant. On the contrary, it is purely physical, and depends mainly upon the mutual relations of the substances (membranes and solutes) which the conditions bring into contact.

It must be evident that the solutes which diffuse into the plant, but which are not metabolized, nor removed from solution in any way, would not accumulate in the plant beyond the attainment of an equilibrium of that solute between the cell sap of the plant and the soil solution. However, if some tissue in the plant uses a certain solute, or changes it chemically, or precipitates it from solution, thus disturbing the equilibrium of the solute, that particular substance would tend to diffuse toward the point of disturbed equilibrium, if the membranes were permeable to it. Such used solutes may be looked upon as selected, but the "selection" is by the cells that make use of the materials or disturb the equilibrium. The roots, for instance, exert no selective action toward supplying just such salts as the plant needs; they will admit anything that other parts of the plant use.

Of course, not every problem of solute intake can be explained on the principle of disturbed equilibrium. For instance, it has been observed that *Nitella* or *Valonia* cells may take in chlorides, bromides, etc. from a dilute solution containing these solutes, until the cell sap contains fifty to one hundred times as much of these salts as does the surrounding liquid. There is as yet no adequate explanation for these unusual cases, and they cause us to question the adequacy of our theories of solute intake and migration. Light seems to be necessary for the process of accumulation[1] in some cases.

3. TURGOR AND ITS CONSEQUENCES

Immigration of water. — The general principles of water immigration have been discussed under osmosis and osmotic pressure. The part which the internal solutes play in producing water intake and turgor must now be considered. The fact that there are formed within the cells certain organic substances, sugars, asparagine, organic acids, etc., to which the cytoplasmic membranes are nearly impermeable, and that they may accumulate to a considerable extent, insures the entrance of water into such cells either directly from the outside or indirectly from adjacent cells in which the solutions are less concentrated. These organic solutes, produced and retained by the protoplasts, are the main cause of the continuing unbalance of water molecules on opposite sides of the membranes. Wherever these organic

[1] Hoagland, D. R., Hibbard, P. L., and Davis, A. R. The influence of light, temperature, and other conditions on the ability of *Nitella* cells to concentrate halogens in the cell sap. *Jour. Gen. Physiol.* **10**: 121–146. 1926–7.

substances are most concentrated in the cell sap, there the water molecules are farthest apart, or least concentrated, or less free from hydration forces, and water flows in from the outside, or from cells with a higher water diffusion pressure. After the water has entered the cell, these solute molecules may interfere with the outward migration of water, and solute diffusion may hamper the diffusion of the water in all directions. The ordinary mineral salts have little part in creating unbalanced conditions in the plant cells except as they modify colloidally bound water, for they penetrate the membranes rather readily, and have about equal effects on the distribution of water by diffusion migration in the various cells. The conditions determining the movement of the water, then, are created mainly by the number and nature of the *organic* solutes present in the cell sap. But the motive power of water immigration resides in the kinetic diffusion pressure of the water molecule itself.

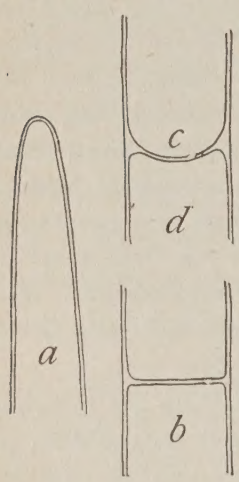

FIG. 6. — The cell walls of a *Cladophora*: *a*, young tip of a filament; *b*, a division wall in the middle of a filament; *c*, a division wall next to a dead cell (*d*). In *b* the pressures on opposite sides of the cross wall are equal, and the wall straight; whereas in *c*, the living cell with osmotic pressure, presses the wall toward the dead cell, *d*, which exerts no pressure.

Turgidity. — As a consequence of the migration of water into the vacuole, the protoplast is forced outward against the cell wall, which, being elastic, is stretched thereby, unless the pressure is balanced by an equal pressure from an adjoining cell. Superficial cells, without exception when healthy, have the free wall convex outward. The filamentous algae have the free end often very convex (fig. 6, *a*), but the partitions between cells at a little distance from the end are practically plane (fig. 6, *b*). If the filament be broken or a cell dies, the adjacent walls, previously plane, at once bulge out (fig. 6, *c*) on account of this internal pressure. When a cell is surrounded on all sides by those of equal internal pressure, its walls are plane.

The condition of cell walls in a massive tissue may be comprehended clearly by inspecting a mass of bubbles such as may be formed by blowing air through a tube into a soap solution.[1] The outer bubbles will have a convex surface, but plane

[1] This may be made of a plain glycerine soap. More durable bubbles may be made from this solution: Shaved white Castile soap 10 gm. by weight; warm water 400 cc.; dissolve. To 15 parts by volume, add glycerine 11 parts. This will be improved by allowing it to stand for a week, cooling over night to 3° C. and filtering cold until limpid.

films divide the air bubbles in the interior. Pricking a superficial bubble gives opportunity for the plane walls of those adjacent to it to bulge, because the internal pressure is now unbalanced.

A cell thus overfilled with water, with the elastic wall stretched, or under strain and ready to stretch, is said to be *turgid*, as was noted in the discussion of osmotic pressure, and the condition is designated as *turgidity*. Manifestly, turgidity depends upon two factors: the presence of a solute or solutes in sufficient amounts, and an adequate supply of water; the solutes produce lack of water equilibrium between the cell and its environment and the water outside must be free to enter the cell.

Turgor pressure and osmotic pressure. — These two terms are rather difficult to distinguish. Osmotic pressure is the pressure of water flowing through a membrane in response to an unbalanced condition of the forces that cause water movement, on opposite sides of the membrane. These forces include kinetic water diffusion, electroendosmose, chemical hydration forces, etc., all of which help to produce the pressure of water across the membrane. The pressure developed within the cells when an adequate supply of water is at hand may reach the theoretical value determined by these forces, mainly by the osmotic concentration of the solutes to which the cytoplasm is impermeable. Obviously the osmotic concentration exists, with the potential capacity to produce pressure, whether or not it can actually exhibit itself. It can exhibit itself only when enough water is present to produce the pressure. A drying cell may have a high osmotic concentration, but be suffering severe plasmolysis.

When water is present abundantly, the internal pressure exhibits itself by the distention of the cell, and the stretching of the elastic cell wall. This particular phenomenon is called turgor,[1] or turgor pressure. Thus we can speak of both osmotic pressure, and turgor pressure in the cell. As the pressure within the cell increases in the presence of water, the protoplasm may become more permeable and begin to allow the liquid to leak through the membranes before the theoretical values of the osmotic pressure have been reached. This leakage sets a limit, then, to the actual pressures which can be produced, and this actual pressure is the turgor pressure. The osmotic pressure, however, is the pressure of the inflowing water, which would reach the theoretical limits if leakage did not occur. Turgor pressure

[1] The term is not always thus restricted; it is often used as synonymous with turgidity.

under these circumstances is seldom as great as the theoretical osmotic pressure.

Thus, in the cells of the sugar beet, the cane sugar alone has an osmotic pressure of 10 or 11 atmospheres; and there are certainly many other solutes which would add greatly to this. But the turgor pressure can only reach a point at which water will filter through the cytoplasm and cell wall, and this is probably less than half the osmotic pressure of the sugar alone.[1]

That the unbalanced condition of water-moving forces in the cell is always ready to produce turgor in the cell in the presence of abundance of free water is shown by the fact that flaccid cells placed in pure water quickly become turgid.

Ursprung [2] has criticized the loose use of the term osmotic pressure in discussions of water relations. He prefers to call the forces which carry water into the cell "suction force," a very unsatisfactory term, and claims that the total power of the cell to obtain water is the difference between the "suction force" of the contents of the cell, minus the oppositely directed wall pressure of the turgid, stretched cells. In a cell that is entirely filled with water, but not in turgid, stretched condition, "suction force" and osmotic pressure would be about the same thing. We should keep clearly in mind the fact that cells *do not suck in water*, but that the water goes into the cell by its own kinetic power of diffusion.

Plasmolysis. — If a turgid cell is placed in a solution so concentrated with solutes that it contains less water per unit volume than the cell sap, water emigrates from the cell, which then becomes more or less flaccid. By measuring turgid cells, or making careful camera drawings of them, comparison after treatment with an appropriate solution shows the shrinkage of the wall to its unstretched size. If the outside solution still has less water per unit volume after a loss of water from the cell just sufficient to permit the return of the wall to its unstretched condition, water continues to leave the cell. As a consequence of the diminished volume of cell sap in the vacuole the protoplast draws away from the wall, if this is rigid enough (as it often is) to support itself; or if not, the whole cell, wall and all, is collapsed. Usually only extreme shrinkage from loss of water, resulting in separation of proto-

[1] Further studies of this subject are much needed, especially as the usual mode of testing osmotic pressure by plasmolysis has been shown to be faulty.

[2] Ursprung, A. Dürfen wir die Ausdrücke osmotischer Wert, osmotischer Druck, Turgordruck, Saugkraft synonym gebrauchen? *Biol. Zentrolbl.* **40**: 193–216. 1920.

plast from wall, is called plasmolysis; but obviously, plasmolysis has two phases, inseparable except arbitrarily. It begins with the first emigration of water, and up to the complete recovery of the cell from previous stretching, it can be detected best by measurement. In its second phase the further emigration of water is made evident by the more or less extensive collapse of the protoplast. The principles governing plasmolysis are those which apply to osmosis in general. The water leaves the cell whenever there are fewer molecules in contact with unit area of its membranes outside than inside. If one thinks in terms of the *concentration of the water* on opposite sides of the membrane, and the *diffusion of water in accordance with its own distribution*, the nature of plasmolysis of plant cells in strong solutions of salts is quite clear.

Rigidity from turgor. — The emigration of water which takes place when a turgid cell is surrounded by a solution containing less free water than the cell sap, is only one way by which turgor is reduced or plasmolysis produced. The evaporation of water may produce the same effects. When a flexible organ, like a leaf or a young shoot, loses water to such an extent that its cells are no longer turgid, the parts bend by their own weight; the edges of the leaf and the tip of the shoot droop. To the touch they are less rigid than before. This observation shows one effect of turgor. Thin-walled cells in masses, such as form the greater part of young shoots, leaves, and young roots, are rendered much more rigid by the strains set up in the mass by turgor. Turgor tensions in the smaller and in the less differentiated plants, as well as in the younger parts of all plants, are thus important in maintaining bodily form; whereas in the older parts, especially of large plants, mechanical tissues, characterized by thickened and altered cell walls, provide the requisite rigidity.

Growth and turgor. — Besides its rôle in maintaining bodily form, turgor has important relations to the growth of cells, especially in the phase when enlargement is the marked feature (see p. 205). At this time water is entering in relatively large amount, and turgidity is prerequisite to the permanent enlargement. The cells of flaccid tissues do not grow larger. Whether stretching is merely a mechanical necessity for such growth, or whether growth is dependent upon the increase in solutes, which would likewise determine the increase in turgor, or whether both conditions are necessary, is not certainly known. The earliest stages of growth of the cell are mainly an in-

crease in the quantity of new protoplasmic material, which has been called growth by accretion.[1] The later enlargement phase accompanied by the development of the vacuole and osmotic action, is known as growth by distention.

Sap pressure and turgor. — Turgor plays an important part also in "root pressure" (see p. 95), by reason of which, under certain conditions, water is forced by the cells of the cortex into the conducting tissues, whence it may escape by filtering through the walls, or directly if these are cut or broken. Further, it is probable that turgor is indispensable for the excretion of water and various solutes from superficial cells. But this may be treated better in connection with the topic secretion (p. 82).

Turgor and movement. — Certain of the movements of plants, such as the opening and closing of the leaflets of Mimosa, and the photeolic movements of legumes, Euphorbia, and other plants, are brought about by rapid changes in the turgor of cells in special motor organs. Some of the movements formerly described as tropisms may really be turgor movements. Thermotropism of roots, curvature in response to temperature differences, has been shown to be a turgor movement.[2] The relation of turgor to movement will receive detailed discussion later. (See Sec. 6, Chapter V.)

4. THE PERMEABLE REGIONS OF ROOT AND SHOOT

Plants and water. — Most if not all of the simpler algae and fungi, many of the liverworts and mosses, practically all submerged plants, and the young stages of even higher land plants are readily permeable to water and to various solutes in every part of the body. In such case they must grow in water or in very damp places. For, if water may be readily admitted over the whole surface, it may be almost as readily lost from the whole surface; it will evaporate whenever the air in contact with any part of the surface is not saturated with water vapor, and this is the usual condition.

Terrestrial plants. — The earliest plants on the earth's surface, it is likely, were aquatic; and in the course of time plants developed that were adapted to temporary exposure on the shore rocks or along the

[1] MacDougal, D. T. Hydration and growth. *Carnegie Inst. Pub.* No. **297**. 1920.
——— The distentive agencies in the growth of the cell. *Proc. Soc. Exp. Biol. and Med.* **19** : 103–110. 1921.

[2] Eckerson, Sophia. Thermotropism of roots. *Bot. Gaz.* **58** : 254–263. 1914.

beaches, then to longer exposure and drier ground, until the land finally was occupied by plants which are so constructed that they can expose a large part of the body continually to moist though unsaturated air. The deserts even, with only a meager rainfall, are by no means barren of vegetation, but support hosts of plants, which are able to secure the scanty moisture from the soil and to avoid in the growing season excessive evaporation into the very dry and often very hot air to which they are exposed. The prime requisite to terrestrial life is some means of reducing the evaporation from aerial parts to an amount which can be replaced by the water entering those parts of the body that remain in contact with it.

The root system. — The members of the higher plants constantly in contact with water pertain chiefly to the root system.[1] Of the root system, however, only the younger parts are permeable to water, since with age the surface cells become altered, or usually are underlaid and finally replaced by corky or cutinized tissues, whose walls are nearly waterproof. But as the roots are growing at the tips and branching, there are always young and permeable parts.

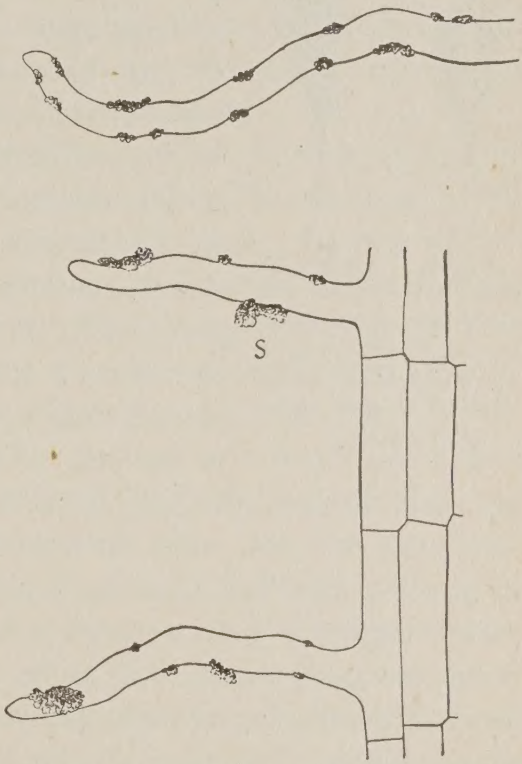

FIG. 7. — Root hairs of lettuce, with adherent soil grains (*s*). Root hairs are really much longer and narrower than the figures indicate. They are usually 1.5–3.0 mm. long, and only about 0.015 mm. in diameter. They are therefore 100–200 times as long as they are thick.

Root hairs. — The surface cells of the young root in most land plants, at a short distance behind the growing apex, branch, sending out tubular extensions, the root hairs (fig. 7), which push their way among the soil particles, displacing some and being deformed by crowding against others, to which they often adhere strongly. These root hairs increase 5–30-fold the permeable area of the root, and by their size and radial position come into immediate contact with a

[1] In some plants the underground stems and leaves (scales) are also in contact with water, but they are almost impermeable to it, and hence may be neglected in this connection.

cylinder of soil 3–8 mm. in diameter (fig. 8). They anchor the young root thoroughly, since they adhere so firmly to the soil particles that they tear away from the root when that is pulled out of even the loosest soil; and if by chance they come away, they bring with them the adherent grains. The root hairs are transient, not living through even one growing season. They die away on the older parts of the roots, from which the hair-bearing cells usually slough off; but new hairs are being formed continually, during the growth of the root in length, just behind the advancing apex. The chemical nature[1] of the walls of root hairs is of considerable interest. Their walls are chemically similar to the middle lamella of the cell walls throughout the plant body. This middle lamella was described in the early pages of this chapter as a pectic layer. It is, indeed, mainly composed of calcium pectate, a salt of pectic acid with calcium. This calcium pectate root hair is lined within by a very thin, protoplasmic layer, surrounding a part of the vacuole of the cell. The pectic walls and the protoplasm are both hydrophile colloids, with great imbibitional attraction for water in the soil. The intimate attachment to the soil particles brings the root hair into contact with the soil water films, and the whole organ is well adapted to bring about the initial steps of water intake by roots. In some cases, of course, cellulose and callose are found also in the walls of root hairs, outside or inside of the pectic layers; but very frequently only the pectic substances are found. St. Popesco[2] thinks the root hairs are not the main organs of absorption, but that absorption is more closely connected with the region of elongating cells just below the root hair zone. (See *Ecology*, Vol. III, for variation of root hairs and for kindred topics.)

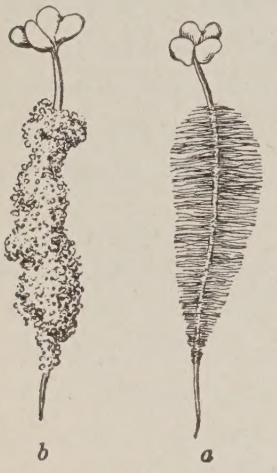

FIG. 8. — Seedling of mustard; *a*, grown in moist air; *b*, grown in sand and withdrawn to show mass of soil grains clinging to root hairs. — After SACHS.

Soil. — The soil, into which roots clothed with root hairs spread, consists of particles of weathered or comminuted rock of various kinds, usually mixed, especially in the upper part, with more or less organic

[1] Roberts, Edith A. The epidermal cells of roots. *Bot. Gaz.* **62** : 488–506. 1916.
Howe, Caroline. Pectic material in root hairs. *Bot. Gaz.* **72** : 313–320. 1921.

[2] St. Popesco, Dr. Recherches sur la région absorbante de la racine. *Bul. Agr.* **4** : No. 10–12. 1926.

matter, the offal of antecedent animal and plant life and living organisms, including algae, bacteria, protozoa, and fungi. The soil particles are of various sizes and kinds, and the soil is often named accordingly. Thus there are gravelly, sandy, clayey, and humus soils according to the amount of gravel, sand, clay, or humus present. An indefinite variety of mixtures also occurs, as in loam, with appropriate descriptive names. The texture of the soil depends chiefly upon the size of the individual particles; but when very fine, and especially when repeatedly wetted and dried, these often become aggregated into compound grains, as is obvious in clay. The sort of rock from which the soil was made, the size of the particles, their state of aggregation, and the proportion and character of organic matter, determine the relation of water to the soil, and so the freedom and extent of its movement.

Soil water. — Of the water which falls upon the surface as rain all may percolate into the soil, or part may run off. The character of the soil and of the vegetation on the surface, the slope, the rate of precipitation, and the existent water content, determine the fate of the falling water. A loose dry soil of level surface, a soil cover of leaves or grass, and a gentle rainfall, tend to reduce the run-off to a minimum. The water which percolates into the soil enters the spaces between the soil particles, which it fills more or less, driving out the air and adhering in the form of films to the component particles, when it does not fill the spaces completely. The thicker the films, the less firmly the molecules more distant from the surface of the soil particles are held; so that gravity suffices to carry down to lower and lower levels a certain amount of the percolating water. This may drain away as subterranean streams or may remain, saturating the soil at a certain level and forming thus the "ground water table," approximately parallel to the surface and at a variable distance from it.

Classification of soil water. — The water of the soil has been classified in various ways. The water that sinks freely in response to gravitation is called gravitational water. That portion of the water held by the soil constituents against the force of gravity includes the capillary water and hygroscopic water. The water which will freely evaporate is the capillary water, while the water still remaining in the soil when it is air dry is called hygroscopic moisture. Still more minute classification has been attempted on the basis of the amount of water that can be frozen in the soil at different temperatures.[1]

[1] Bouyoucos, G. A new classification of soil moisture. *Soil Sci.* **11**: 33–47. 1921.

That which can be frozen at − 5°C. is called " free " water, and that which cannot be frozen is called unfree, or bound, water. Evidence of various kinds indicate that there are no fundamentally different kinds of water in the soil.[1] It all acts alike in evaporation and colloidal hydration, and can serve as solvent for the soil minerals. The classification into gravitational, capillary, and hygroscopic water is satisfactory for ordinary purposes.

Capacity of soils for water. — When all the water that will sink to the ground water table in a well-drained soil has drained out of the upper regions, an amount varying according to the physical characters of the soil remains, adhering to the grains. This is the capillary water mentioned above. The smaller spaces are still filled; the larger contain bubbles of air which have come in from above as the water sank. If the soil particles be very small and close together, a greater quantity of water will be held than in a loose, coarser soil.

This seems anomalous, but as the amount of water adhering to the surfaces will be almost proportional to the surfaces themselves, it may easily be comprehended by calculating the area of 1000 spheres each 1 mm. in diameter, which could be packed into a cubic centimeter, in contrast with the area of 1,000,000 spheres each 0.1 mm. in diameter occupying the same place. In the first case the area would be 3141.6 sq. mm; in the second, ten times as much, or 31,416 sq. mm.

In coarse soils, therefore, such as sand, water largely drains away; whereas in fine soils, such as clay, it is held, and it may be so firmly held as to preclude the admission of more, once the soil is saturated; whence a layer of clay often forms a " hard-pan," in which water collects as in a basin, or over which it runs. Humus soils hold much water, because the particles of organic matter, besides being covered by the usual films, are not only porous, thus admitting water to the interior spaces, but are also able to imbibe it by their very substance.

Soil water constants. — The value of soils for economic purposes varies with their water-holding power, and various methods have been developed for comparing the water-holding capacity of various kinds of soils. Moisture capacity is the absolute dry weight basis percentage of water held by a soil against the force of gravity.

[1] Keen, B. A. The evaporation of water from soil. *Jour. Agr. Sci.* **6** : 456–475. 1914, and *Jour. Agr. Sci.* **11** : 432–440. 1921.

Russell, Sir E. J. *Soil Conditions and Plant Growth.* 5th ed., pp. 353–362. Longmans, Green & Co. 1927.

Of more value to the physiologist are such constants as the moisture equivalent, wilting coefficient,[1] and hygroscopic coefficient. These constants are useful in studying the relation of vegetation to soil water. The moisture equivalent may be defined as the percentage of water held by a soil against a centrifugal force 1000 times larger than the force of gravity, applied for about 40 minutes. This measure is obtained by use of specially designed soil centrifuges.

The wilting coefficient is the percentage of moisture left in the soil at the time a plant wilts permanently in it under moderate conditions of evaporation. This constant is about the same for all kinds of plants in any given soil, because it depends more upon the physics of the soil water than upon the plant. At the wilting point, the soil films of water have become so thin and immobile that water delivery from soil to plant almost ceases. Under these circumstances, almost any plant will wilt before the extremely slow rate of delivery can change much the percentage of water left in the soil. Measurement of the surface forces in soils[2] shows that the water left in the soil at wilting is held with a force of about 4 atmospheres. And although plant roots have an average osmotic concentration of about 8 atmospheres, they are still unable to secure the soil water because it no longer moves toward the plant with sufficient speed.

The hygroscopic coefficient is the percentage of moisture held by a soil when in moisture equilibrium with a saturated atmosphere. The finer soils have a larger hygroscopic coefficient than the coarser or sandy soils. The film water of soils at the hygroscopic coefficient is held by a force of about 22 atmospheres.[3] Only quite xerophytic plants can remain alive in soils at the hygroscopic coefficient,[4] and even these cannot *grow* in such dry soils. Methods have been worked out whereby one can calculate the various soil constants from some one determination. Thus, if the wilting coefficient, or the moisture equivalent is known, one can calculate the other constants approximately. (See note [1] below.)

[1] Briggs, L. J., and Shantz, H. L. The wilting coefficient for different plants and its indirect determination. *U. S. Dept. Agr. Bu. Plant Ind. Bull.* **230**. 1911. Also, *Bot. Gaz.* **53** : 20–37. 1912.

[2] Shull, C. A. Measurement of the surface forces in soils. *Bot. Gaz.* **62** : 1–31. 1916.

[3] Wolfe, H. S. Surface forces of soils within the range of hygroscopic moisture. *Bot. Gaz.* **82** : 195–206. 1926.

[4] Alway, F. J. Studies on the relation of the nonavailable water of the soil to the hygroscopic coefficient. *Nebraska Agr. Exp. Sta. Research Bull.* No. 3. 1913.

Capillary ascent of water. — The movement of water through the soil by capillary action is of some importance to the plant, although there is less upward capillary transfer of water than was at one time believed. It can readily be demonstrated that moderately fine soils, like the silty loams, show the largest capillary rise when one end of a dry column of soil is set into water. Sandy soils show a rapid rise, but the distance is not so great. Clay shows a very slow capillary rise, long continued, but frequently not as great as the somewhat coarser silty loams.[1] The latter soils show the most favorable capillary behavior for plant growth.

If equilibrium were momentarily reached among the water films in the soil, it would be upset the moment any water evaporated from the upper grains, for the water film that clothed them would thereby become thinner. This would at once cause a rearrangement of the water in all adjacent films, because the adjacent water particles are pulled more strongly to the places where the film is thin than they are held where it is thick. Thus evaporation from the soil causes, on the whole, an upward movement of the water from the deeper parts of the soil, a disturbance which extends as far as is permitted by the resistance offered by the attraction of the soil particles and by the viscosity of the water. As this effect may reach the water table, the result of evaporation is to lower it; its level rises after heavy rain and falls in prolonged drought. Not all the water which enters the soil can leave it, either by drainage or evaporation, for the hygroscopic water always remains in the soil. Only by heating above 100° C. can all moisture be driven off.

Migration of soil water into roots. — When a root penetrates the soil and root hairs develop from all sides, the entire surface becomes clothed with a film of water just as is the case with the soil grains. When some of this water enters a root hair or any part of a surface cell, the water film becomes thinner and there takes place the same sort of readjustment as is produced by evaporation of water at the surface of the soil, with the same general movement of water, in this case toward the root.[2] In both cases even distant parts of the soil may thus furnish water to make good the loss. All such movements of water, being mass movements and not diffusion movements, involve the transfer of

[1] Hilgard, E. W. *Soils*. pp. 202–207. The Macmillan Co. 1921.

[2] Shull, C. A. Absorption of water and the forces involved. *Jour. Amer. Soc. Agron.* 22 : 459–471. 1930.

any solutes present; whence it comes that solutes from a distance may be brought into the vicinity of a root and may enter it if the conditions permit. But inasmuch as the mineral solutes in the soil waters are very similar, no matter what the character of the soil may be, this is probably of less importance to the plant than it would seem to be at first sight.

Available water. — By no means all of the water in the soil is free to migrate into the roots. There comes a time, as the films about the soil particles become thinner and thinner, when the adhesion of the water to the soil grains is equal to its diffusion tension. Leading up to that equilibrium, it grows increasingly difficult for the plant to balance its loss of water by that entering; its cell sap has become more and more concentrated; and when the outgo surpasses permanently the income, permanent wilting usually ensues and often more or less extensive death of the foilage.

The available water of a soil, so far as plant growth is concerned, is the water represented by the difference between the water capacity of the soil and the wilting coefficient. At any given moment, of course, the available water is that in excess of the wilting coefficient. The wilting coefficient in sand may be less than 0.5 per cent, in loams 10 to 12 per cent, in clays 15 to 20 per cent, and in muck soils possibly as high as 20 to 25 per cent. The water capacity of these soils varies also. It is about 15 per cent for sand, 40 to 65 per cent for loams and clays, and from 100 to 120 per cent for mucks. These figures indicate roughly the possibilities as to available water in the different types of soils.

Effect of roots on soil. — A considerable amount of carbon dioxide (CO_2) and less quantities of other substances diffuse from the root into the soil-water films. Solution of carbonates is increased by the presence of CO_2 in water, as is shown by the readiness with which a polished marble plate may be etched by roots traversing its surface and giving off CO_2. Reactions due to other solutes which diffuse from the root, or to excretions from it, may determine the solution of other sorts of soil particles, and the substances so dissolved may then enter the root. It is not known that these changes so produced in the soil are of any considerable importance in plant life. Whether by diffusion from the roots of live plants or by the decomposition of dead roots, or by both, it is certain that various complex organic compounds exist in soils, which may interfere seriously with the growing of plants thereon. Nearly

fifty of these organic compounds of the soil have been isolated and identified. Among them quite a number have been found to be toxic to plants, as for instance dihydroxystearic acid,[1] α-crotonic acid,[2] and salicylic aldehyde.[3] In certain soils the character and quantity of these substances are so injurious that the soils are almost sterile. Even a watery extract from them proves harmful. In such cases the soil can be improved by mechanical and chemical treatment designed to remove or destroy the harmful compounds. The rotation of crops may find partial explanation herein; the excretions and decomposition products of a given crop may be injurious to the same plants, but less so or not at all to others. Even manuring may prove to have its value less in the compounds put into the soil than in the improvement of soil texture and the destruction of the deleterious compounds in it.

Oxidizing power of roots. — The roots of plants possess the power to oxidize certain organic compounds,[4] and it is believed that they may oxidize some of those toxic constituents found in soils. Usually oxidation of an organic toxic body changes it to a non-toxic substance, as there are so few toxic compounds in comparison to the number of those which are non-toxic. This oxidizing power is possible because of the presence of an organic catalyst in the root cells, an enzyme, called *peroxidase*. This enzyme brings about the oxidation process, and may thus exert a protective function against these injurious decay products in the soil. Bacteria, by decomposing and oxidizing such toxic substances in the soil, also exert a favorable influence on plant growth.

Entry of water. — The cells bearing root hairs and the adjacent ones are so constructed as to facilitate the immigration of water and various solutes. The cell walls are thin and the protoplast apparently forms only a thin sheet over the inner surface, the greater part of the cell being occupied by a huge sap cavity. The cell sap usually contains more solutes than the water outside; the internal diffusion pressure of

[1] Schreiner, Oswald, and Shorey, Edmund C. The isolation of harmful organic substances from soils. *U. S. Dept. Agr. Bu. Soils*, Bull. **53**. 1909.

Shorey, E. C. Some organic soil constituents. *U. S. Dept. Agr. Bu. Soils*, Bull. **88**. 1912.

[2] Walters, E. H., and Wise, Louis E. α-crotonic acid, a soil constituent. *Jour. Agr. Res.* **6**: 1043–1045. 1916.

[3] Skinner, J. J. Soil aldehydes. *Jour. Franklin Inst.* **186**: pp. 165–186, 289–316, 449–480, 547–584, 723–741. 1918.

[4] Schreiner, O., and Reed, H. S. The rôle of oxidation in soil fertility. *U. S. Dept. Agr. Bu. Soils*, Bull. **56**. 1909.

the water is consequently less, and water enters, distending the cell until the elastic recoil of the stretched wall is sufficient to balance the osmotic pressure of the solutes, or to exude as much water as enters.

Entry of solutes. — At the same time, if any solutes to which the protoplast is permeable exist in the soil water, but either not at all or in less amount in the cell sap, they will diffuse into the cell. But their movement is as independent of the movement of the water as are the conditions of such movement; *water and solutes move independently.* If any solute which enters thus is not changed or stored in the plant, *i.e.* if it is not removed *as such* from solution, it may attain equilibrium inside and outside the plant, so that no more enters; but if it is removed by being chemically changed or by being stored, more constantly enters.

Entry and exit *via* roots. — The root therefore possesses permeable surface cells always in contact with soil water, through which water and a variety of solutes, chiefly oxygen and mineral salts, make their way, under the conditions already set forth regarding osmosis. At the same time, the root permits through these same surfaces the outgo of any solute formed in the cells, to which the cytoplasm is permeable, that does not exist at equal or greater pressure in the soil water. It is even conceivable that water would pass out thus, were it possible for the soil to become sufficiently dry. Artificially this can be demonstrated; it has not been shown that it occurs in nature. When the roots are exposed to air, as in transplanting, especially if the plants are to be transported far, it is necessary to guard against excessive loss of water by evaporation from the roots; and the quick drying of exposed roots is a most obvious danger in transplanting.

Mineral nutrients. — The mineral solutes in the soil solution provide the plant a source of calcium, potassium, magnesium, iron, phosphorus, sulphur, manganese, nitrogen, iodine, boron, zinc, and possibly other elements, required for the developmental physiology of the plant. Each of these elements plays some very important part in the life processes, and if the soil is deficient in one or more of them, they become limiting factors in plant production. Intelligent fertilizer practice should be based upon a thorough knowledge of the functions of each element in the plant, and the consequences of starvation for the necessary nutrients. It would be useless, for instance, to use an ordinary N, P, K fertilizer to overcome lack

of calcium, or sulphur, or magnesium. The functions of each of the important mineral elements will now be considered.

Calcium. — This element plays a very important part, both in the plant and in the soil. In the plant it helps to form the calcium pectate middle lamella which cements the cells of the plant body together, and it probably forms in the protoplasm, calcium soaps and calcium proteinates, which are believed to have much to do with maintenance of the normal semipermeability of the plasmatic membranes, ectoplast and tonoplast. In the complete absence of calcium, plants not only cannot take in the other needed mineral nutrients, but also allow those salts which have been taken in to leach out through the roots into the surrounding medium.[1] The harmful action of distilled water[2] has been traced in part to this leaching effect, caused by the absence of calcium. So this element may be said to make all the other elements available to the plant. Calcium also unites with free oxalic acid in the tissues, forming calcium oxalate crystals, and preventing overacidity in the cells. It also affects the general tone and vigor of the plant, and aids root growth. When the calcium supply becomes deficient, as, for instance, in a solution or sand culture with only ten parts per million of calcium in the solution, growth ceases, the meristem regions of stem tips die, probably because there is not enough calcium to permit division of the cells, formation of middle lamellae, calcium proteinates, and soaps in the new cells.

In the soil or solution culture, calcium exerts an antitoxic action toward substances which, if used alone, would injure the plant. Thus *Vaucheria* is easily killed by placing it in a dilute solution of sodium chloride. But if a small amount of calcium chloride is added to the solution, the plant is protected from the toxic sodium salt.[3] This antitoxic action of calcium has been observed in connection with a good many harmful compounds.

Calcium in the form of lime is much used to overcome soil acidity. Much of our agricultural land is now acid and in need of lime applications. In some states three fourths of the arable land would be improved by being limed. This need is increasing each year, for it has been discovered that the Mississippi River carries out to sea in solution

[1] True, R. H. Significance of calcium for higher green in plants. *Science* **55** : 1–6. 1922.

[2] ———. The harmful action of distilled water. *Amer. Jour. Bot.* **1** : 255–273. 1914.

[3] Osterhout, W. J. V. Extreme toxicity of sodium chloride and its prevention by other salts. *Jour. Biol. Chem.* **1** : 363–369. 1906.

and suspension more than 20 million tons of calcium, annually.[1] This loss comes mainly from the deeper soil layers, as the surface layers are already severely leached. Calcium is also useful in breaking up soils that are too heavy and sticky, such as gumbo soils. In some way, either by modifying the electric charge on the colloidal clay particles, or by coagulating the surface coating of silicic gel material,[2] the clay particles are flocculated, which means that they collect into compound grains. A flocculated soil has good tilth, and is easily broken up; it is looser, drains better, has better aeration, and is warmer. The conditions for functional root activity and root development are greatly improved in such soils by the use of lime. It must be clear that calcium is one of the very important mineral solutes in the life of the plant.

Potassium. — This element, like calcium, is useful in forming metallic proteinates in the protoplasm, and may be a stimulant to protoplasmic activity, as it possesses some photo-electric properties. Probably it is necessary for complete division of the cells. The general tone and vigor of the plant depend in part upon potassium, for one finds that plants are more resistant to the effects of bad seasons, insects, worms, and fungus diseases when the soil is adequately supplied with potash.

Deficiency of potassium harms the leaves of plants producing characteristic white spots in some cases, and in others causing them to die back from the tips; moreover, it greatly reduces the amount of food which the plant can manufacture and store. Whether this is due to an interference with the sugar manufacturing process, or with the transportation and storage of food is not definitely known, but it is probably the transportation process that is slowed down; for sometimes high starch content is found in leaves of potash-starved plants. It has also been shown recently that the phloem vessels, which are the main channels of translocation, undergo some degeneration during severe potassium starvation. This evidence favors the idea that it is the translocation that suffers rather than manufacture of food.[3] At any rate, root and grain crops are greatly reduced by too low

[1] McHargue, J. S., and Peter, A. M. The removal of plant-food by natural drainage waters. *Kentucky Agr. Exp. Sta. Bull.* No. **237**. 1921.

[2] Comber, Norman M. The mechanism of flocculation in soils. *Trans. Faraday Soc.* **17** : 349–353. 1922.

[3] Johnston, E. S., and Dore, W. H. *Plant Physiol.* **4** : 31–62. 1929.
Hartt, Constance E., *Bot. Gaz.* **88** : 229–261. 1929.

potassium supply, and it is mainly the storage regions, roots and seeds, that remain small or shriveled.[1]

The unconsolidated soils of the south-eastern Atlantic coastal plain have been so depleted of potassium by heavy rainfall that large quantities of potash fertilizer must be used in that region. Almost half of the kainite imported into our country is used in four or five of the south Atlantic states. North and South Carolina, Georgia, Alabama, and Florida are mainly in need of potash fertilizers, but any soil may become deficient in potash.

Magnesium. — The main function of magnesium in the plant is in connection with the building of the green pigment, chlorophyll. Each molecule of chlorophyll contains one atom of magnesium, and the ash from pure chlorophyll consists of pure magnesium oxide. When magnesium is deficient in the soil, plants may become abnormally yellow because of unhealthy chlorophyll. This diseased condition is called *chlorosis*. It has been recently discovered that the disease known as "sand drown" is a magnesium chlorosis,[2] which can be overcome by application of magnesium salts.

Magnesium is probably related also to the process of oil formation, as certain plants which normally store food as oil droplets do not form them in the absence of magnesium. It is also found that oily seeds have a higher magnesium content than starchy seeds.

Magnesium by itself may be toxic. It does not require a very strong magnesium nitrate solution, for instance, to inhibit or retard root development. Calcium readily overcomes the toxic action of magnesium salts.

Iron. — In some unknown manner iron is related to the development of chlorophyll, although it is not a constituent of the chlorophyll molecule, as is magnesium. Absence of iron induces a marked chlorosis or yellowing of the leaves. While iron is usually present in soils in sufficient amounts, it is sometimes in a very insoluble condition, unavailable to the plant. This unavailability of iron is sometimes caused by excessive supply of calcium or manganese in the soil. In Porto Rico and in certain areas in the United States, the iron is rendered insoluble by calcium carbonate. Plants grown on such areas are chlorotic, but

[1] Russell, E. J. *Soil Conditions and Plant Growth*, 5th ed., pp. 84–89. Longmans, Green, & Co. 1927.

[2] Garner, W. W., McMurtrey, J. E., Bacon, C. W., and Moss, E. G. Sand drown, a chlorosis of tobacco due to magnesium deficiency, and the relation of sulphates and chlorides to the disease. *Jour. Agr. Res.* **23** : 27–40. 1923.

they can be cured by spraying the foliage with a solution of iron sulphate.[1] In Hawaii similar troubles are encountered in connection with the manganese soils of that region.[2] Spraying with solutions containing iron salts overcomes the difficulty. The iron may be related to the general respiratory function of all cells,[3] while the deficiency may become visible only in the chlorophyll-containing cells.

Phosphorus. — Protoplasm, especially the nuclear material, contains phosphorus as one of the building constituents. The phosphoproteins, phospholipins, phytins, etc., cannot be formed without the presence of this element. It is probable that lack of phosphorus would interfere with nuclear division in meristem regions. The soil usually contains only small amounts of phosphorus, but there are notable exceptions, such as the soils of central Kentucky. Soils rich in phosphates grow the highest quality crops and develop animals with the finest bone. In France the best vineyards grow on soils rich in phosphates. Abundant supplies of phosphorus seem to hasten ripening of grains and to stimulate depth of root growth.

Sulphur. — Proteins are made up of acids known as *amino-acids*, joined together to form very complex molecules. Two of these amino-acids contain sulphur. One of these, cystein, contains one atom of sulphur, and the other, called cystine, contains two atoms of sulphur. All proteins except the protamines, whether obtained from plant or animal sources, give a positive test for the presence of sulphur. Therefore sulphur is necessary for the formation of the great majority of the proteins. A substance has been recently discovered and named *glutathione*, which is related to these sulphur-containing amino-acids. Glutathione is an autoxidizable body,[4] one capable of taking up oxygen from the air, which it may then yield to other bodies for purposes of oxidation. In other words, it may function in some important way in respiration. It is the sulphur-containing groups which give glutathione its remarkable properties.

[1] Gile, P. L. Relation of calcareous soils to pineapple chlorosis. *Porto Rico Agr. Exp. Sta.* Bull. **11** : 1–45. 1911.

Korstian, C. F., Hartley, C., Watts, L. F., and Hohn, G. G. A chlorosis of conifers corrected by spraying with ferrous sulfate. *Jour. Agr. Res.* **21** : 153–171. 1921.

[2] Johnson, M. O. The spraying of yellow pineapple plants on manganese soil with iron sulfate solutions. *Hawaiian Agr. Exp. Sta.* Press Bull. **51** : 1–11. 1916.

[3] Warburg, O. Iron, the oxygen carrier of respiration ferment. *Science* **61** : 575–582. 1925.

[4] Hopkins, F. G. On an autoxidizable constituent of the cell. *Biochem. Jour.* **15** : 286–305. 1921.

In addition to these protein constituents, many plants contain mustard oils, which cannot be formed without sulphur. This is especially true of the plants belonging to the family *Cruciferae*.

Sulphur, then, is an important building element in all plants. It also stimulates root growth in some cases, and is of greater importance in the life of plants and animals than ordinarily supposed.

While sulphur is not very abundant in soils, and is probably decreasing in many,[1] it has become a limiting factor in only a few. In the states of Washington and Oregon,[2] the soils are so deficient in sulphur that very large increases in yield may be obtained by applications of calcium sulphate, or other sulphur-containing minerals. While sulphur is rather easily removed from soils by drainage water, there is also return of sulphur to the soil in the rainfall [3] and in the acid phosphate and manures used as fertilizer. The decrease of sulphur in the soil, therefore, is usually slow.

Manganese. — While manganese has usually not been named as a necessary element for plant growth, evidence is accumulating [4] to show that plants grow better if not deprived entirely of this element. The special function of manganese is not very clear, but it has been said that the respiratory enzymes, the oxidases, require the presence of manganese for their activity. Manganese is said to be the coenzyme of oxidase although iron may so function. Neither manganese nor oxidase is supposed to be able to carry on oxidation alone, but both together can carry on the oxidative processes. If this is a correct interpretation of the function of manganese, it is evident that manganese should be considered an essential mineral nutrient. A chlorosis of spinach [5] was found to be caused by lack of manganese, and was overcome by additions of this element.

Nitrogen. — Like phosphorus and sulphur, nitrogen is a building element of proteins. It helps to form all of the amino-acids, and is so characteristic of the proteins that they are often called nitrogenous substances. But not all nitrogenous substances are proteins. The

[1] Woodard, John. Sulphur as a factor in soil fertility. *Bot. Gaz.* **73** : 81–109. 1922.

[2] Reimer, F. C., and Tartar, H. V. Sulphur as a fertilizer for alfalfa in southern Oregon. *Oregon Exp. Sta.* Bull. **163** : 1919.

[3] Eaton, S. V., and Eaton, J. H. Sulphur in rainwater. *Plant Physiol.* **1** : 77–87. 1926.

[4] McHargue, J. S. Manganese and plant growth. *Jour. Ind. Eng. Chem.* **18** : 172–175. 1926.

[5] McLean, F. T., and Gilbert, B. E. Manganese as a cure for chlorosis in spinach. *Science* **61** : 636–637. 1925.

soil nitrogen is contained mainly in humus, which serves as a storehouse of nitrogen in organic form, and as atmospheric nitrogen in the air spaces of the soil. Both of these kinds of nitrogen must be converted into soluble nitrogen compounds, mainly nitrates, before they are useful to the plant.

With deficient soluble nitrogen, plants have a dull green color, a starved appearance. On the other hand, an abundant supply of nitrogen produces a dark green healthy growth of vegetation, which is tenderer and more juicy than if grown with a smaller supply. Such tissues are often more readily attacked by insects and fungous diseases. If the soil is too rich in nitrogen, the plants tend to remain green too long, and to produce excessive vegetative growth without much fruit or food storage. On such soils tomatoes and potatoes may form enormous vines, but produce almost no fruits nor tubers. Leaf crops like lettuce and cabbage are favored by very rich soils, but are usually too tender to withstand shipment when grown on such soils.

Nitrification. — Neither humus nitrogen nor atmospheric nitrogen as such can be used by ordinary plants. Both are in unavailable form, and must be made available by chemical change. The process by which unavailable humus nitrogen is converted into available nitrates is called *nitrification*.

Nitrification, which is carried on largely by bacterial action, involves several steps. The first step of the process is the general decay of the proteins of the humus, whereby they are hydrolyzed or digested. The proteins are thus broken down into their constituent amino-acids by the decay of bacteria. Then the nitrogen of the amino-acids is changed to ammonia by the action of organisms known as ammonifying bacteria. The ammonification reaction may occur in more than one way. First, the amino-acids may be oxidized. The reaction is as follows:

$$\underset{\text{(amino-acid)}}{CH_3 \cdot CHNH_2 \cdot COOH} + O_2 \longrightarrow \underset{\text{(fatty acid)}}{CH_3 \cdot COOH} + CO_2 + NH_3$$

Here the carbon atom to which nitrogen is attached is oxidized to form CO_2, and NH_3 is split off. Secondly, the reaction may involve the use of H_2O instead of O_2. The reaction would then be represented as follows:

$$\underset{\text{(amino-acid)}}{CH_3 \cdot CHNH_2 \cdot COOH} + H_2O \longrightarrow \underset{\text{(hydroxy fatty acid)}}{CH_3 \cdot CHOH \cdot COOH} + NH_3$$

In this case the NH_2 group is replaced by OH, and the NH_3 is liberated. The final result of either of these reactions is the formation of ammonia from the nitrogen of the amino-acid.

The ammonia is volatile, and would escape from the soil were it not for the fact that the ammonia combines at once with water and carbonic acid to form ammonium carbonate which is nonvolatile.

This ammonium carbonate is used by certain bacteria as a source of energy. They are known as the *Nitrosomonas* group of bacteria, and they oxidize the NH_3 to NO_2, or nitrite. Then the nitrite serves in turn as a source of energy for the *Nitrobacter* or nitrate group of bacteria. They oxidize the NO_2 compounds to NO_3, or nitrates, which can be absorbed and used by plants in general. Nitrification merely converts the unavailable nitrogen of decaying proteins into an available form. It does not increase the nitrogen of the soil. Indeed, nitrification may lead to loss of nitrogen from the soil; for whereas the decaying proteins do not appreciably leach from the soil, the nitrates do readily leach away in the drainage water. Therefore it is well to have plants growing on the soil at the time nitrate is likely to be formed abundantly in the soils. The roots will absorb the nitrates and prevent leaching.

Nitrogen fixation. — The bacteria which convert humus nitrogen to nitrate have no power to act upon the atmospheric nitrogen in the air spaces of the soil. However, there are other bacteria in the soil which can assimilate the atmospheric nitrogen. These are called nitrogen-fixing bacteria, and the process is called *nitrogen fixation.* This fixation really involves the nitrogen metabolism of the bacteria, which are able in some way to build their proteins from the atmospheric nitrogen supply. When they die, their bodies become part of the organic storehouse of nitrogen in the soil, to undergo nitrification and provide nitrate for the higher forms of plants. There are two different groups of these bacteria, one of which lives free in the soil, and the other mainly in tubercles on roots of various legumes. The free-living forms are *Clostridium* and *Azotobacter*, etc., while the nodule-inhabiting form has been known as *Pseudomonas radicicola.* Sometimes these two groups are distinguished as non-symbiotic and symbiotic nitrogen fixers.

The non-symbiotic, free-living forms slowly build in their bodies the organic nitrogenous compounds of the protoplasm. The steps of the process are unknown. By their work they actually increase the

amount of nitrogen in the soil which may become available for higher plants.

The symbiotic bacteria [1] live in the soil and enter the roots of legumes mainly through the root hairs. After entering the root hairs by burrowing through the delicate membranes, they grow in the form of an infection thread into the cortical cells of the root. Here they cause increase in number and size of cells, hyperplasia and hypertrophy, thus causing the nodules to form. In the cells of these nodules or tubercles, they live and feed upon the carbohydrates and other food supplies of the cells of the host plants. Under the rich nutritive conditions prevailing in these nodule cells, the bacteria undergo a degeneration or involution, forming V and Y shaped organisms. In this degenerate condition they utilize atmospheric nitrogen to construct their complex nitrogenous proteins. Ultimately a part of this protein material is rendered available to the legume for its own growth, and legumes are unusually rich in nitrogen, because they have this source of bacterially fixed nitrogen to draw upon. When the legumes are harvested, their roots and portions of their stems may be turned under the soil. Through the processes of decay the fixed nitrogen in the legume becomes available to other plants through nitrification.

Each type of legume seems to have a slightly different strain of bacteria on its roots,[2] and if any given soil lacks the proper strain for the particular legume we desire to cultivate, we can now practice inoculation of the soil with the proper strain. It is best to use forms that have already been grown on the legume of the desired kind. The best way to inoculate is to treat the seeds with a culture of the bacteria, and then plant the seeds without allowing them to become very dry. In England they use skimmed milk largely as an inoculation medium, as it provides better food for the bacteria while making their start in the new soil environment.

Denitrification. — There are some bacteria in the soil, like *Bacillus denitrificans*, which can break up nitrogenous compounds in such a way as to set nitrogen free in gaseous form.[3] They thus reverse the process of nitrogen fixation. These organisms are called denitrifying bacteria. They would cause much harm in soils were it not for the

[1] Greaves, J. E. *Agricultural Bacteriology*. chap. xxiv. Lea and Febiger. 1922.

[2] Burrill, T. J., and Hansen, R. Is symbiosis possible between legume bacteria and non-legume plants? *Illinois Agr. Exp. Sta.* Bull. **202**: 113–181. 1917.

[3] Greaves, J. E. *Agricultural Bacteriology*. Denitrification. chap. xxii. Lea and Febiger. 1922.

fact that they are mainly anaerobic, requiring the absence of oxygen for rapid multiplication and activity. The general management of land is therefore unfavorable to these forms. The aeration of the soil by plowing and drainage naturally favors the aerobic nitrification and nitrogen fixation bacteria, and represses the denitrifiers.[1]

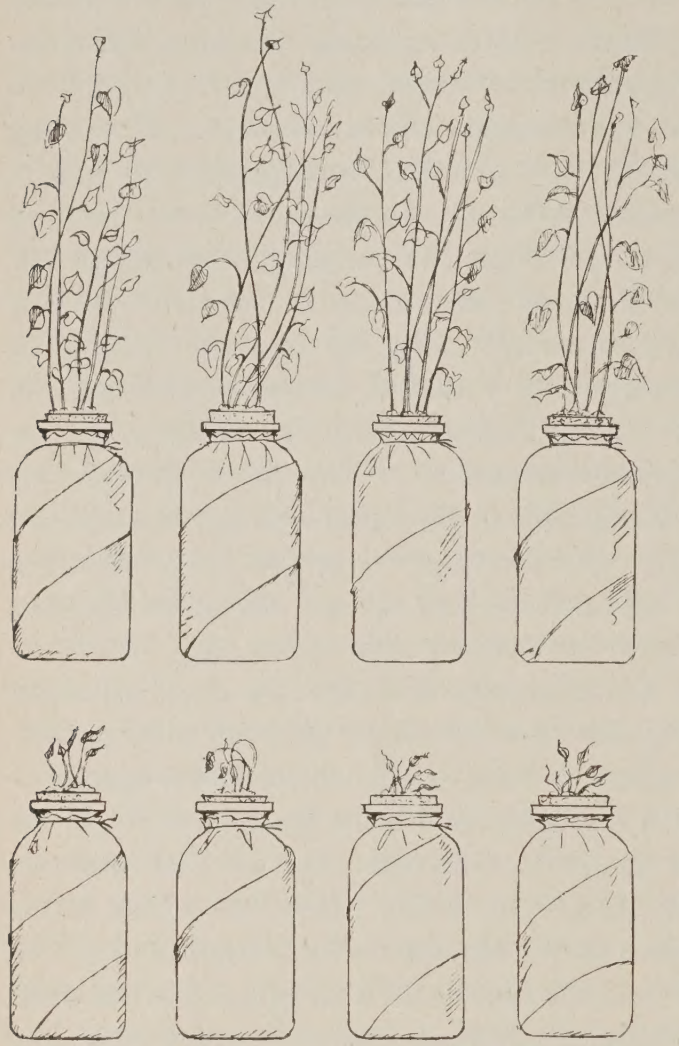

FIG. 9.—Influence of boron on growth of buckwheat. The nutrient solutions are in pyrex bottles, and the buckwheat seeds were germinated on perforated corks in a dust-free room. The upper row of cultures had ½ part per million of boron, the lower row had none. Both have grown the same number of days. — Redrawn from Fig. 5, Sommer and Lipman, *Plant Physiology*, 1 : 237, 1926.

Other necessary elements. — In addition to the eight elements here considered, and C, H, and O, there are others which plants must have, at least in small amounts, or they cannot grow and fruit normally. Until recently it was not discovered that such elements as iodine,[2] boron, zinc, and copper are indispensable to many kinds of plants. (See fig. 9.) It was not discovered because the amounts needed are so small. One part of boron to two million of soil, that is, one pound to the acre, is enough to permit good growth.[3] Our previous experiments were not carefully enough planned to exclude these elements, so their part in healthy growth

[1] Greaves, J. E. *Agricultural Bacteriology*. Denitrification. chap. xxii. Lea & Febiger. 1921.

[2] Stoklasa, J. Die physiologische Funktion des Jods beim Bau- und Betriebsstoffwechsel in der chlorophyllhaltigen und chlorophyllosen Zelle. *Biochem. Zeitschr.* **176** : 38–61. 1926.

[3] Sommer, A. L., and Lipman, C. B. Evidence on the indispensable nature of zinc and boron for higher green plants. *Plant Physiol.* 1 : 231–249. 1926.

was not discovered. In addition to these, it has been claimed that aluminum, silicon, sodium, and possibly chlorine are necessary for plant growth. Certainly, no experiments have ever yet been carried on in which these elements were entirely excluded; so it is impossible to state definitely just which elements are necessary. The functions which these elements may have are obscure. They may be related to the catalysts of the living cells, or may actually help to build vital parts of the protoplasm. Since they are never very deficient in the soil, they are not likely to become fertilizer problems.

One of the elements mentioned, iodine, is of special interest; for there are areas in this and other countries where the soil does not contain enough iodine to give plants the proper iodine value in the nutrition of animals. Where the vegetation lacks iodine we are likely to have many cases of goiter among humans, and other derangements of metabolism among animals. In such cases, vegetables grown on iodine-treated soils would help to prevent derangement of animal metabolism.[1]

Adsorption of ions. — The root hairs, in contact with the soil particles, form the permeable region of entry for all of these needed elements, as well as for the water of the soil. The soil particles, by virtue of their small size and chemical composition, tend to hold the various solute ions on their surfaces by means of physical and chemical forces which are sometimes referred to as surface forces. The ions of the soil solution are said to be *adsorbed* by the soil particles, and held, some more strongly than others. Such ions as PO_4, NH_4, and K are held rather firmly in the soil, and Ca and Mg not so strongly. But SO_4, NO_3, and Cl are held either very weakly or not at all. The latter ions, therefore, leach out of the soil more readily than the others, although all of them are found in the drainage waters. Adsorption is advantageous in holding fast some of the ions which are added to the soil as fertilizers. The adsorbed ions are held on the surfaces of the soil particles where contact with the permeable root regions of the plant is readily established.

The physico-chemical surface forces which cause adsorption may be closely related to the forces that hold atoms together in the lattice structure of crystals.[2] The unsatisfied secondary valences of the very small colloidal particles of the soil seem to attract ions to their surfaces in

[1] Hart, E. B., and Steenbock, H. Hairless pigs. — The cause and remedy. *Wisconsin Agr. Exp. Sta.* Bull. **297**. 1918.

[2] Millard, E. B. *Physical Chemistry for Colleges*, pp. 100–103. 1921.

much the same way that they would take up material in crystal growth. In some cases, the charge of the ions may play a part. The clay colloids are usually negatively charged when in water, and they may attract the positive ions more strongly than the negatively charged ions.

Soil colloids. — The material which brings about adsorption in the soil is in a very fine state of subdivision, as has just been noted. It is so finely divided that it is in colloidal condition. The colloidal fraction of the soil is very important with respect to the physical properties of the soil. The water capacity of the soil, the value of such important soil constants as the hygroscopic coefficient, the plasticity, and tilth, are determined in some cases largely, in others almost wholly, by this colloidal material. The student should consult several of the general books on the colloidal state of matter.

There are two kinds of colloidal matter in the soil: (1) that which is derived from purely mineral sources, and (2) that which arises from the decay of vegetable and animal matter. Plastic qualities of soils depend mainly on the mineral colloidal substances, while tilth and fertility depend more largely upon the black organic humus colloids. Both are related to the water relations of the soil. Control of the amount of humus in the soil gives us the best means of improving the water-holding capacity of agricultural soils.

The mineral colloidal fraction has been carefully investigated in recent years. By means of a supercentrifuge it has been separated out from the rest of the soil, and subjected to analysis. It is found to contain nine or ten oxides of bases, mainly silicon dioxide and aluminum oxide.[1] These two oxides form about 75 per cent of the mineral colloidal fraction. The other oxides are those of iron, magnesium, potassium, calcium, titanium, and manganese. Some phosphorus and sulphur oxides also occur. The silica is the most important, and exists mainly as a film on the tiny particles of soil. The flocculation of clay soils by lime is believed to be caused by the coagulation of the surface coating of silica gel on the surfaces of the particles. The particles then clump together and form aggregates, which crumble readily and exhibit what we commonly call tilth. It is also believed that Ca, which carries two positive charges of electricity, may neutralize the clay particles, which are usually negatively charged, and cause them to precipitate at the isoelectric point.

[1] Robinson, W. O., and Holmes, R. S. The chemical composition of soil colloids. *U. S. Dept. Agr.* Bull. **1311** : 42. 1924.

The humus colloids [1] are derived mainly from the cell wall structures of plants. During decay the celluloses, lignins, and particularly the dead bodies of bacteria, break down in such a way as to produce a residue of black material, the humus, that remains permanently in the soil. As far as we know, the protein residues of higher plants play little or no part in the formation of humus, but are mainly important as a source of nitrate production. In addition, the protein reserves give rise by decay to certain phenolic compounds, and other similar bodies, which would be toxic if not oxidized. As we have already seen, both the roots of plants and bacteria of the soil decompose these compounds rapidly into harmless constituents.

The dark color of forest top soils, and the darker color of nearly all surface soils as contrasted with the subsoils beneath, is caused by the gradual accumulation of this residue of organic humus. Aldehydes and organic acids of various kinds have been found in this colloidal humus fraction, some of which may help to cause soil infertility. Thus, dihydroxystearic acid has been credited with retarding the growth of plants where it occurs in unusual amounts, and α-crotonic acid caused infertility in a local Texas soil. Crop rotation, and proper aeration through drainage and cultivation, which favor the oxidation processes mentioned, usually suffice to prevent overaccumulation of the harmful products of decay.

Base exchange in soils. — When the colloidal materials of the soil are treated with a solution of some salt, as $CaCl_2$, or KCl, some of the basic ions of the salt are taken up by the colloids, and other basic ions are liberated from the colloids into the solution. This exchange of basic ions is spoken of as " base exchange." The property of basic exchange is a characteristic of both the mineral and humus colloids of the soil. The mineral colloids have a zeolitic constitution. They are produced by a chemical union of the various oxides mentioned in the preceding paragraph, to form a complex substance, somewhat crystalline in structure, as is shown by X-ray diffraction studies. This complex which is capable of base exchange contains many different basic ions, Ca, K, Mg, Na, Fe, Al, H, and NH_4 being the main ones. The humus colloids also contain basic ions, as in the case of calcium humates, potassium humates, etc.

Soil fertility is dependent in part upon the nature of the basic ions

[1] Waksman, S. A. *Principles of Soil Microbiology*, pp. 689–696. Williams and Wilkins. 1927.

which predominate in this colloidal complex. A fertile soil usually has a large amount of replaceable calcium in its colloidal fractions. As soil is cultivated, if no fertilizers are added, there is a tendency for hydrogen to enter the complex and replace such ions as Ca, K, Mg, etc. When the base exchange complex comes to have hydrogen as its predominant base, the soil is an acid soil, and needs to be treated with lime and other basic fertilizers to restore the balance of basic metallic ions in the base exchange complex. If for any reason sodium becomes the predominant base in the mineral colloid, the soil is an alkaline soil, due to the formation of Na_2CO_3, and should be given treatment that will tend to restore it to neutrality.

It has recently been shown that the base exchange complex will yield much more exchangeable magnesium if it is ground up to a very fine state. The more it is ground, the more magnesium it will yield in exchange. The magnesium is probably held in the complex by secondary crystalline valencies, which are broken by the fine grinding, thus bringing a larger proportion of the magnesium ions into the surfaces of the particles produced by the grinding. It is evident, from a study of crystal structure, that internal ions are held by six bonds, while those in surfaces, or along edges, or at corners of the crystal are held by five, four, or three valencies respectively. The less firmly the ions are held, the more readily they can be exchanged in this process known as base exchange.

It seems probable that the taking up of basic ions from the soil colloids by the roots of plants involves base exchange. The plant may, for instance, give up some hydrogen ions to the soil colloid, and thus liberate Ca or K or some other needed basic element, which could then be absorbed into the plant tissues through the roots. The nature of base exchange has been understood only a short time, and many of the relationships must be carefully investigated before the full significance of the phenomena can be grasped. It must be clear, however, from this discussion that base exchange is a very important feature of soil behavior, and that it is related very closely to the problems of maintenance of soil fertility. Fertilizer management of soils will probably become much more scientific as the facts concerning base exchange are more fully developed.

Aërial permeable regions. — Land plants possess also certain permeable regions on the aerial parts of the shoot. Small plants that grow in wet places, where the air is very moist or nearly saturated, might

safely have all aërial parts permeable, because evaporation is slow and the distance from root to aërial surface short. Moreover, spray or rain falling on such parts may enter there, as well as soil water by the roots. But larger plants could not exist in ordinary dry air were their permeable aërial surfaces freely exposed; for if accessible to rain, the evaporation would be dangerously great. So far as protection is concerned, large plants with aërial shoots might thrive (1) if they were completely waterproofed, thus checking all evaporation, or (2) if their damp surfaces were shielded by drier partial coverings, thus reducing evaporation and necessarily excluding water.

Waterproofing *vs.* salts. — There seems to be no *a priori* reason related to the necessary supply of water and salts why the first of these alternatives should not have appeared in small land plants. Structurally, it would be quite possible to waterproof the aërial parts completely, since plants do check water loss by such means in certain places. In such a case, enough water for other purposes might undoubtedly enter, since enough to supply the great evaporation now enters by the roots alone. But, it is objected, this would have prevented the intake of sufficient salts. As to that, it is not probable that stopping evaporation, and therefore the inflow of water at the roots, would interfere with the supply of salts in small plants. This is rendered probable, because diffusion of solutes is independent of the movement of water; and to assume, as this objection does, that the solutes are carried along by the entering water which replaces that evaporated, contravenes all that is known about osmotic movement. The fact that plants grown in the sun where evaporation is very rapid may actually take in less salts than plants of the same kind grown in partial shade emphasizes the independence of water and solute movement into the plant.[1]

In tall plants, however, it is not at all probable that diffusion alone could supply the necessary solutes to the top of the plant. If it requires five or six weeks, as has been claimed, for salts to diffuse ten or twelve inches, when the gradient for diffusion is produced by saturation at one end of the column of solvent and zero concentration at the other, it would require many years for salt molecules to reach the top of a giant sequoia or Australian eucalyptus, with such gradients of diffusion as exist between soil and plant. Complete waterproofing

[1] Hasselbring, Heinrich. The relation between the transpiration stream and the absorption of salts. *Bot. Gaz.* **57**: 72–73. 1914.

of plant surfaces exposed to the air would probably have set a definite limit upon the height to which land plants could grow.

The fact that the luxuriant rain forests of Ceylon and other tropical regions can develop in climatic conditions which reduce evaporation to a minimum, should not lead one to believe that these plants can be supplied with sufficient solutes by diffusion unaided by other processes. These trees may continue to lose water vapor even during a rain; and there are always some periods when rain ceases long enough for salts to be distributed to the tops of the tallest rain forest trees by mass movements set up by evaporation.

Waterproofing *vs.* gases. — Even if water and salts were admitted, a complete waterproofing of aërial surfaces would exclude the gases of the air, because all substances must enter in solution. So, as a matter of fact, plants possess aërial surfaces of large extent, freely permeable, but shielded by covers which, while more or less waterproof, are perforate, so that gases have access to the moist cells underneath. There is one gas, oxygen, needed by almost every plant for respiration, which the terrestrial plants can get satisfactorily only from the atmosphere. There is another gas, carbon dioxide, which is absolutely essential for the food making of green plants, and this likewise can enter land plants in sufficient amounts, only from the air. Small amounts may enter through the roots in solution in the soil water, but roots usually excrete CO_2. As the food made by green plants is the sole supply for them and for most other living things, even for man, and further is the chief source of energy for doing the world's work,[1] it is evidently of some importance that the aërial parts of green plants should expose wet surfaces to the air and so make possible the solution and admission of oxygen and carbon dioxide.

Protective tissues. — The admission of oxygen and carbon dioxide by the smaller plants, mosses, liverworts, and the like, is made possible by the fact that the whole surface of the body is moist and therefore permeable. But the larger plants expose wet cell walls only as the bounding surfaces of internal chambers that constitute an aërating system, shielded by a nearly waterproof epidermis or a layer of cork tissue. The outer wall of the epidermis has its outermost layer so completely cutinized[2] as to constitute a continuous sheet, the cuticle; and the subjacent layers are often infiltrated with cutin to a greater or

[1] Spoehr, H. Photosynthesis. chap. i. Chemical Catalog Co. 1926.
[2] Priestly, J. H. Suberin and cutin. *New Phytologist* **20** : 17–29. 1921.

less extent. Besides this, the epidermal cells not infrequently form wax, resin, and similar substances which are secreted in granules or continuous sheets on the outer wall. These substances all repel water, so that only minute amounts occupy these parts of the wall; consequently very little can escape into the air as vapor. On the older parts of the stem, the epidermis is at first underlaid, and later, sloughing off, is replaced by layers of cells, which, before losing their living contents, impregnate the walls with suberin, so that they become nearly impermeable to water (*cork*). Both these superficial waterproof tissues, epidermis and cork, are perforate at numerous points (stomata and lenticels), which communicate with and indeed form a part of the aërating system.

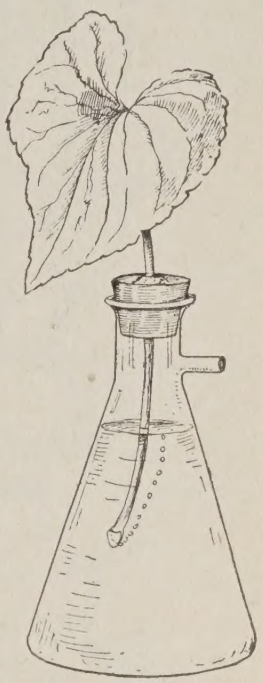

FIG. 10. — Demonstration of the continuity of the leaf and cortical intercellular aërating system. The gases escape from the cortex. The vascular elements may also emit some air bubbles, but only from expansion of gases in the tracheae.

Aërating system. — This is a network of canals and intercellular spaces, of the utmost irregularity in land plants, and connected throughout. The continuity of the aërating system can be demonstrated easily by sealing a leaf with a long petiole through the stopper of a side delivery flask in such a way that the petiole is partly submerged in water. (See fig. 10.) On producing a negative pressure in the flask by suction, bubbles of air may be seen rising from the cut end of the petiole. The air enters the leaf blade through small pores called stomata, and travels through the continuous network of spaces in the blade of the leaf and cortex of the petiole, following paths of least resistance, until it emerges where the system was broken by removal of the leaf. If the position of the leaf is reversed, so that the blade of the leaf is under water, the negative pressure now draws bubbles of air through the stomatal pores over the general leaf surface, wherever they happen to be distributed. They appear first from the largest stomata which offer the least resistance to air flow. The intercellular passages are formed gradually among the parenchyma cells by partial separation as they enlarge. At first all cells are coherent with their neighbors, a necessity of the mode of division; but unequal growth and turgor produce strains which split the common wall at the corners and sometimes

along whole faces (fig. 11.) In submersed water plants the aërating system attains its most marked development; huge canals arise in the softer tissues of the stems and leaf-stalks (fig. 12), and in other parts branched cells, the branches in contact only by their tips, leaving large space for gases. These inner chambers in submersed aquatics do not communicate with the atmosphere directly; they

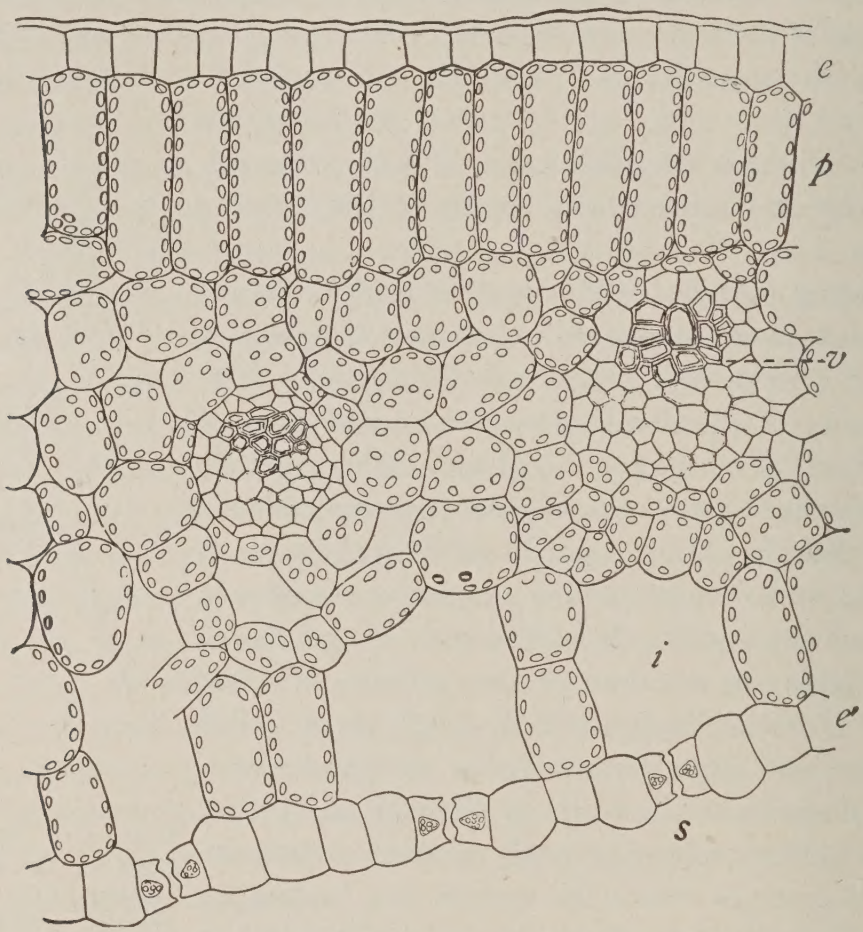

FIG. 11. — Cross section of leaf of lily, somewhat diagrammatic: *e*, upper epidermis; *e'*, lower epidermis, with stomata, *s*, in cross section; *p*, palisade; between *p* and *e'*, spongy tissue, with large intercellular spaces (*i*) below stoma (*s*) and vein (*v*).

contain gases which have come out of solution in the adjacent cells and constitute an internal atmosphere into which gases may diffuse or from which gases may migrate into the living cells (of course in solution).

Stomata. — The aërating system of the terrestrial plants, and of water plants not normally completely submersed, communicates with the atmosphere freely, because certain cells of the epidermis, predetermined by the mode of their development, break apart through the

central portion of their last-formed division wall. As immediately beneath them an air space of some size develops, this establishes a passage to the outer air. These two crescentic cells of the epidermis are the lips of a mouth-like slit called a *stoma;* the two lips are called *guard cells* (fig. 13). The guard cells differ from other epidermal cells in their crescentic form and smaller size, and in having chloroplasts, which are usually absent from other epidermal cells. Their walls are also peculiarly and unequally thickened. Their turgor variations, the unequally thick walls, and their position with respect to the adjacent cells make them change shape, with increasing turgor becoming more arcuate and, with lessening turgor, straighter. The mechanism of stomatal movement is discussed in Chapter II. The effect of these changes is to widen or narrow the slit between them, so making more free or restricted the passage of gases either by flow or diffusion.

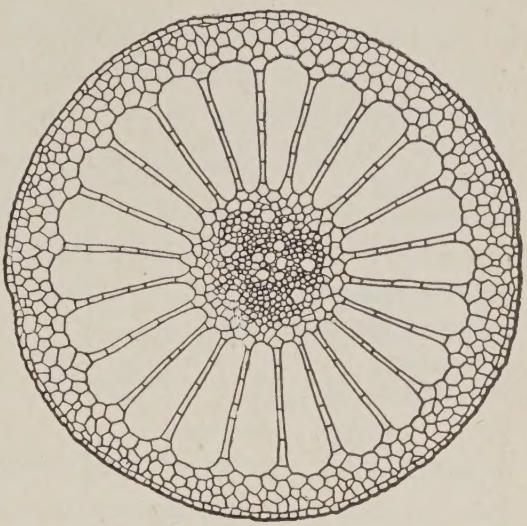

FIG. 12. — Cross section of stem of *Myriophyllum*, with air canals.

Size and number of stomata. — A stoma is very minute; the area of the pore when open, in thirty-seven sorts of cultivated plants, averages 0.000092 sq. mm. But their great number on those organs (such as leaves) in which the admission and exit of gases is most free, makes up for their small size. Both features will be grasped better by this statement: in an area equal to that of the dot here printed (●), there are on the under side of the apple leaf over 1400 stomata, and on the under side of the olive leaf about 2000. The following table (after Weiss) shows the numbers per square millimeter in various common plants.

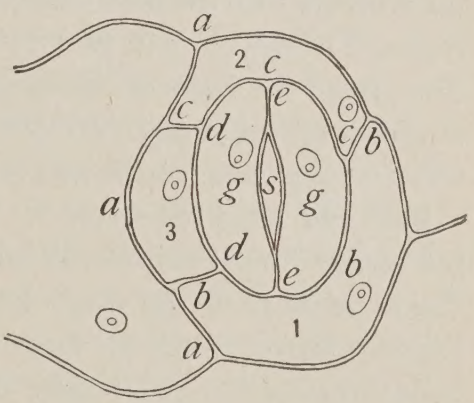

FIG. 13. — Stoma of *Sedum; a, a, a,* first wall, cutting off mother cell of stoma; *b, b, b,* second; *c, c, c,* third; *d, d,* fourth; *e, e,* final wall; the latter, forming the two guard cells, *g, g,* partially splits to form the slit (*s*); 1, 2, 3, subsidiary cells.

Name of plant	Number of stomata		Name of plant	Number of stomata	
	Upper Side	Under Side		Upper Side	Under Side
Olea europaea (olive) . .	0	625	Zea Mays (Indian corn) .	94	158
Castalia odorata (white water lily)	460	0	Betula alba (white birch)	0	237
Helianthus annuus (sunflower)	175	325	Berberis vulgaris (barberry)	0	229
Syringa vulgaris (lilac) .	0	330	Populus deltoides (cottonwood)	89	131
Solanum Dulcamara (bittersweet)	60	263	Pinus Strobus (white pine)	142	0
Pisum sativum (pea) . .	101	216	Avena sativa (oats) . .	48	27
Ficus elastica (rubber plant)	0	145	Lilium bulbiferum (tiger lily)	62	62

So far as plants have been examined, it appears that a large majority of mesophytes have less than 200 stomata to the square millimeter, and a fair average is perhaps 150.

Transpiration. — Since the intercellular spaces are bounded by moist cell walls, freely permeable to water, they are always filled with air which contains more or less water vapor. This vapor diffuses through the stomata into the drier outer air, and being lost from the plant will be replaced in whole or in part by water entering the root. At the same time, since the walls of the epidermal cells contain a little water, some evaporation takes place directly from them. The total evaporation of water under these conditions is designated as *transpiration* (see p. 60).

Exit and entry of water. — The leaves and other aërial parts of plants are almost constantly losing water by evaporation, because the vapor pressure of the water held by the cell walls is greater than the vapor pressure of the air most of the time. At the same time there is little opportunity for intake of water by the leaf, even when it is deluged. The cuticle of the leaf, waxy in nature, is only slowly permeable to water. Just as water can slowly evaporate through the cuticle, so it can enter slowly through this structure. Thus if a young wilted burdock leaf, with its petiole sealed with wax, is arranged with the blade submersed in water, the leaf recovers its natural crispness without taking water in through the stomata. Careful weighing of the wilted leaf and of the turgid leaf after removal of all surface water, may show in 24 hours 25 per cent increase in weight from water taken

in through the cuticle. Water enters the leaf through the stomata only when a partial vacuum has been produced in the intercellular spaces following submersion.

Although it is possible for the leaf to take in a little water through its cutinized surfaces, in general the leaf presents a structure which renders water loss easy, and water intake much more difficult. The intake of water through the leaf surface is not sufficient to aid materially in the revival of wilted plants after the foliage is sprinkled. Such intake as does occur helps the plant just that much; but the recovery under these circumstances is mainly brought about by checking evaporation from the surface while the roots go on absorbing water from the soil, thus relieving the saturation deficit of the cells which was responsible for the wilting.

Entry and exit of gases. — The aërial parts facilitate the entry and exit of gases. The external atmosphere communicates freely with the internal atmosphere of the intercellular spaces by way of the stomata. Any oxygen or carbon dioxide in the air of the intercellular spaces may dissolve in the water of the cell walls and then migrate into the adjacent cells, if the pressure of these solutes is less in the cells than in the internal atmosphere. In like manner either may diffuse into the internal atmosphere when the reverse conditions exist. The solubility of CO_2 and O_2 in water under like conditions is very unequal, the former being about 30 times as soluble at ordinary temperatures as the latter. The rate of diffusion is also unequal. The quantity of each used or produced by the plant likewise differs. These factors all play a part in determining the amount of gas which enters or leaves. As the composition of the internal air fluctuates on account of subtraction or addition of CO_2 or O_2, a difference is created between the internal and external atmosphere, which leads at once to diffusion through the stomata in a direction determined by the existing inequality in pressure of either gas.[1] Nitrogen, the only other considerable constituent of air, is neither used nor produced; hence practical equilibrium between the N_2 of the air and the N_2 in solution in the plant is early attained, and this equilibrium is scarcely disturbed thereafter. Certain plants, notably cotton, produce an odorous substance, *trimethylamine*,[2]

[1] Further discussion of the rôle of these gases will be found in the sections on Photosynthesis and Respiration.

[2] Power, F. B., and Chestnut, V. K. The odorous constituents of the cotton plant. — Emanation of ammonia and trimethylamine from the living plant. *Jour. Amer. Chem. Soc.* 47: 1751–1774. 1925.

$(CH_3)_3N$), which has a very low boiling point (35° C.), and which vaporizes into the air as a gas. This gas may escape mainly through the open stomata, as is the case with the normal constituents of the atmosphere, but sometimes such odorous constituents escape from glandular cells of epidermal hairs.

In submersed plants the oxygen and carbon dioxide are dissolved in the water and find admission at any permeable surface, like other solutes.

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CHAPTER II — THE MATERIAL OUTGO OF PLANTS

1. TRANSPIRATION

The term transpiration. — Frequent reference has already been made to the most important outgo of material from the plant body — the water evaporated from the aërial parts. This was long ago called *transpiration*, after the analogy of the exhalation of water vapor from the lungs, with whose movements, however, it has nothing in common.

The evaporation of water from the leaves is one of the important functions of these aërial organs. However, it must not be inferred from this statement that the leaves actively remove water from the plant by a physiological process. There is no evidence for the active secretion of liquid water on the internal cellular surfaces, nor of excretion of water vapor by the living cells. The leaves are entirely passive, the evaporation being caused by the kinetic nature of water itself. We cannot even properly speak of the air as possessing an "evaporating power." If the atmosphere is not fully saturated with water, it may be considered a partial water vacuum, into which the water of the leaf tends to migrate by diffusion. The process of evaporation in the leaf is no different than it is from a sponge or a wet towel. But the *rate* of evaporation is different in plants than in other objects, because of peculiarity of structure. It is justifiable, therefore, to use this special name as a convenient and short term for the expression, the evaporation of water from living plants.

Evaporation. — When a dish of water is exposed to air which contains less water vapor than it could hold under its given conditions of temperature and pressure, more molecules of water will fly out of the water surface into the air in unit time than will pass in the opposite direction from air to water. The volume of liquid in the dish decreases by this process; the water evaporates. The rate of evaporation is determined by the temperature of the water, the temperature, pressure, and movements of the air, and the relative humidity of the air over the dish of water. Decreased humidity, higher temperature, lower pres-

sure, or increased movement increases the rate of evaporation, and vice versa.

The presence of any solutes in the water retards evaporation, for some of the solute molecules lie near the surface of the liquid, where they interfere by their molecular attraction with molecules of water which would enter the surface and escape at that point. The solute molecules also enter the surface of the water, and, being non-volatile, block the way for some of the water molecules to enter the surface. This means that the solute depresses the vapor pressure of the solvent, which will necessarily evaporate more slowly from this cause. Or, these solute molecules may exert a chemical attraction toward the water, whereby some of the water molecules may be held in hydration complexes, not free to evaporate. Thus concentrated sulphuric acid not only does not evaporate any contained water into the air, but continues for long periods to remove water from the air. The principles of dynamic equilibrium apply, of course, to this action.

Again, water adherent to any substance, or imbibed by it, is held by surface forces which tend to retard the escape of the water molecules. As a substance dries out, these surface and imbibitional forces increase slowly until they equal the tendency of the molecules of water to escape, after which a state of equilibrium is maintained between the substance and the atmosphere.

Adhesion and colloidal adsorption. — The water which is a part of the plant body adheres in this way to the particles of cell wall, protoplasm, and its inclusions, with forces which are partly physical and partly chemcial. The whole plant body is made up of colloidal solids which hold water imbibed and adsorbed on the surfaces and within the particles. As a rule, the greater the amount of water in any given substance, the less firmly the water is held. But the forces retaining water depend partly on the nature of the colloidal material. It has been found that the colloids made up of carbohydrates with five carbons in each primary group, that is, the pentosans, and various gums and mucilages which contain pentosans, have a higher water-holding power than the colloids made up from carbohydrates with six carbons to the group.[1] Many succulent plants[2] have developed pentosans internally,

[1] MacDougal, D. T., and Spoehr, H. A. The origination of xerophytism. *Plant World* **21** : 245–249. 1918.

[2] ———, Richards, H. M., and Spoehr, H. A. Basis of succulence in plants. *Bot. Gaz.* **67** : 405–416. 1919.

and owe their water-holding capacity partly to this chemical composition. Similarly, plants which can be hardened to withstand slight freezes develop within their cells colloidal proteins which hold water so firmly that these plants are not frozen at temperatures that would have killed had the plants not been so hardened.[1]

Hardiness of plants against winter killing has some such relation. It has been shown, for example, that the hardiest winter wheats develop more powerful hydrophile protein colloids than the more tender varieties.[2] Grimm alfalfa probably has more hydrophile colloidal matter than the less hardy alfalfas of the great plains.[3] At any rate it is much hardier than other varieties.

The attractions between the water molecules and the colloidal matter of the plant are altered when the plant is killed. Thus, if a living leaf and a dead leaf are placed side by side in dry air, the dead leaf loses its water much more rapidly than the living one, and shrivels in a few hours. Probably this is in large part due to changes which occur in the cytoplasmic colloids at death. There is an aggregation of the colloidal material in coagulation at death, and this probably frees much water from its colloidal union. Some of the internal changes may be caused by the very diminution of the water content itself, as by changes in the amount of water in hydration complexes, and thus at any moment may operate to alter suddenly the rate of water loss.

A somewhat analogous action may be observed in the desiccation of copper sulphate, which exists in several hydrated forms, pentahydrate, trihydrate, and monohydrate. In drying at 50° C. the pentahydrate ($CuSO_4 \cdot 5\,H_2O$) maintains a vapor pressure of 47 mm. (mercury) as long as any pentahydrate remains; then the vapor pressure suddenly drops to 39 mm., that of the trihydrate ($CuSO_4 \cdot 3\,H_2O$). With further desiccation it again suddenly falls, as soon as the trihydrate is all decomposed, to 4.5 mm., the vapor pressure of the monohydrate ($CuSO_4 \cdot H_2O$), and there it remains until all of the water is driven off. In this case there would be at each point a sudden fall in the rate of

[1] Harvey, R. B. Hardening process in plants and developments from frost injury. *Jour. Agr. Res.* **15** : 83–112. 1918.

[2] Newton, R. A comparative study of winter wheat varieties with especial reference to winter killing. *Jour. Agr. Sci.* **12** : 1–19. 1922. Colloidal properties of winter wheat plants in relation to frost resistance. *Jour. Agr. Sci.* **14** : 178–191. 1924.

[3] Steinmetz, F. H. Winter hardiness in alfalfa varieties. *Minnesota Exp. Sta. Techn.* Bull. **38**. 1926.

evaporation. Just such sudden alterations have been observed in transpiration.

Nature of the process. — Transpiration has been much misunderstood and has been assumed to accomplish certain ends in the plant which it does not perform. For instance, it has been assumed that transpiration from the leaves produces an inflow at the roots which sweeps in the needed mineral salts with the water. It has also been assumed to be useful in concentration of the dilute salt solutions brought up to the leaves.[1] These ideas are certainly not justified by the known facts. There are several points of view which can be taken regarding the functions of transpiration, and these points of view will be summarized in the following paragraphs.

Transpiration unavoidable and dangerous. — This point of view assumes that transpiration is purely incidental to the structural arrangement of the plant for exit and entry of gases. It assumes that loss of water offers no advantages and serves no good purpose in plant life. Not only so, but also that if transpiration occurs too rapidly outgo will exceed income, and the plant will ultimately perish. Doubtless, millions of plants die each year because transpiration exceeds the intake of water through the roots for extended periods of time. A loose soil and an exposed situation, sudden extreme evaporation due to a hot dry wind, a blazing sun, or prolonged drought, are causes of death of plants only too well known to farmers in some regions. However, dangerous as evaporation may become when extreme or uncontrolled, this point of view overlooks the obvious advantages and the possible necessity of transpiration for successful life.

That transpiration is unavoidable is quite obvious. In leaving stomatal openings and passageways for ingress and egress of oxygen and carbon dioxide, which must enter and leave the plant through wet cell walls, the conditions leading to water loss were unavoidably brought about. Just as long as the vapor pressure of the plant cell walls is greater than the vapor pressure of the atmosphere, and water permeable membranes exist in plants, so long will transpiration be unavoidable.

Transpiration advantageous. — The main advantage which transpiration is supposed to confer upon the plant is in connection with the salt supply of the aërial organs. It must not be assumed, however,

[1] One popular book for children even speaks of leaves as the plant's "kitchens," where the thin "soups" are boiled down!

that the evaporation of water from the leaves causes the intake of salts by the roots. Such an assumption usually involves reasoning which contradicts both the theory and the facts of osmotic movement of water, and the relation of salts to this process.

In the region of root hairs and root cortex, and in the leaf parenchyma, where we find living cells, water and salts must move relatively independently of one another, each diffusing according to its own gradient in the appropriate direction. This must mean that absorption of water and salts are, in general, independent processes, and that water intake can be increased without a corresponding acceleration of salt absorption. There is, indeed, some evidence favoring the idea that salt intake and water intake are independent in the plant as a whole. It has been shown, for instance, that tobacco plants [1] grown in partial shade, where evaporation was slower, actually took in more salts than the same kind of plants grown in the sun, where the evaporation was greater. Similar data have been reported for white pine seedlings.[2] While this problem needs more investigation, it is probably best to consider water outgo as responsible for water intake, and salt utilization by the cells and tissues as responsible for the salt intake, the water merely providing a pathway for the salt migration. Probably this presents the case as more simple than it really is, for there are still many obscure points regarding salt intake by plants.

There is one clear advantage, however, in the rapid "transpiration stream," as the rise of water through the tracheae is called. Salts moving solely by diffusion move very slowly. The average chemical molecule might move at the average rate of four or five centimeters a week in a perfectly motionless column of water. It might require more than a century for a molecule of magnesium phosphate to travel up the trunk of a 300-foot tree, if it had to make the journey entirely by its own kinetic motion. When we recall that magnesium is needed in the manufacture of every molecule of chlorophyll, we realize the importance of rapid distribution of the salt supply, coming in through the root. It is the transpiration that gives rise to the mass movement of the water in the tracheal system, and in this current the ions and molecules of minerals are swept along just as rapidly as they diffuse

[1] Hasselbring, Heinrich. The relation between the transpiration stream and the absorption of salts. *Bot. Gaz.* **57** : 72–73. 1914. The effect of shading on the transpiration and assimilation of the tobacco plant in Cuba. *Bot. Gaz.* **57** : 257–286. 1914.

[2] Burns, G. P. The relative transpiration of white pine seedlings. *Plant World* **18** : 1–6. 1915.

through the border parenchyma cells which surround the tracheae in the leaf. If this removal of salt from the tracheae takes place as rapidly as the water moves, the salts would rise as rapidly as the water, often several feet per hour. If the salts are removed more slowly than the water, then the salt movement should lag behind water movement. Although more knowledge is greatly to be desired on the relations of water and salt migration in plants, it is clear from this discussion that transpiration is advantageous, particularly in tall plants where distribution of salts would otherwise become a serious problem.

Transpiration necessary? — By some physiologists transpiration is regarded as a necessary process in plant life.[1] This view ascribes to transpiration as its chief function the dissipation of the excess energy which the plant receives from the sun during isolation. That sunlight may injure plants in the absence of transpiration may be demonstrated by exposing plants under a bell jar to the full effect of the sun on a bright day. Plants receive and absorb in their leaves an enormous amount of sunlight energy. There are several ways in which the energy may disappear. A small fraction, probably often less than one per cent, is used in the endothermic manufacture of the carbohydrates. A small amount may be given off into the air if the plant is warmer than the air. This process is called *thermal emissivity*, and involves conduction, convection currents, and radiation of heat into the atmosphere. But the main method of dissipating the sun's energy is by evaporating water. The leaf is very well adapted for this work.

In order to show more clearly why this dissipation of energy might appear necessary, we may consider what would happen if the energy falling upon the leaf should accumulate in the tissues and cause rise in temperature rather than evaporation. How rapidly would the temperature rise? This can be calculated roughly from the facts we know concerning the total energy receipt by the leaf, reflection and transmission of light, and the specific heat of leaf substance.

By means of a radiometer it has been found that approximately 0.8 calorie of energy is received upon each square centimeter of leaf surface in one minute, during bright direct illumination. Not all of this is absorbed, for at least 10 per cent is reflected,[2] and about 25 per cent transmitted. The absorption coefficient would be about 65 per cent,

[1] Shull, C. A. Transpiration as energy dispersal. *School Sci. and Math.* **19** : 1–6. 1919.

[2] ———. A spectrophotometric study of reflection of light from leaf surfaces. *Bot. Gaz.* **87** : 583–607. 1929.

then, which gives 0.52 calorie absorbed per sq. cm. per minute. If this amount of energy accumulated in the tissue, the temperature would rise very rapidly. If the mass[1] of the square centimeter of leaf tissue is 0.020 gm., and the specific heat is 0.879 (water = 1), then the rise in temperature per minute will be obtained by taking the product of mass by specific heat, and dividing it into the absorbed energy. Using the figures given, it is found that the leaf would heat up at the rate of 30° C. per minute. As the killing temperature of many plants is about 60° C., and the air temperature is about 20° C. at the start, it would require considerably less than two minutes to kill the plants, were there no dissipation of energy. It is readily understood why some people believe transpiration is a vitally necessary function, even though the leaf is entirely passive in permitting the energy dissipation. This idea is easily exaggerated beyond its real value, for, as is shown below, thermal emissivity keeps down the temperature of the leaf if transpiration is checked.

Thermal emissivity. — As the plant warms up from the absorption of energy more rapidly than transpiration dissipates it, thermal emissivity comes into play to assist in the removal of surplus energy. Indeed, so efficient is this method of loss that plants rarely exceed the air temperature, even in extreme cases, by more than 10 to 20 degrees. Such temperature excess has been observed in plants such as *Aloe* and *Euphorbia* which show reduced transpiration.[2] Thermal emissivity tends to prevent serious injury in all such plants as have low transpirational loss because of structural modification.

Measurement of water loss. — The amount of water given off by a plant can be measured in several ways. Usually one determines this by weighing potted plants from time to time, having covered the pots with some material impervious to water, either a metal shell, or rubber damask, or a wax seal. In the case of cut off branches, the potometer may be used. This is an instrument which really measures the rate of absorption of water by the cut end of the branch rather than the loss of water from the leaves. If the cut branch is recovering from a saturation deficit during the experiment, the instrument does not give a true reading of the transpiration; and any water used in photosynthesis

[1] Shull, C. A. The mass factor in the energy relations of leaves. *Plant Physiol.* 5 : 279–282. 1930.

[2] Pearson, H. H. W. Observations on the internal temperatures of *Euphorbia virosa* and *Aloe dichotoma*. *Annals Bolus Herb.* 1 : 41–66. 1914.

during the experiment is measured along with the transpirational loss. A very convenient form of potometer can be made by using two burettes, one to contain the plant, and the other for reading off the loss (fig. 14). This instrument permits as accurate work as volumetric quantitative analysis, but has the same defects as the ordinary capillary potometer.

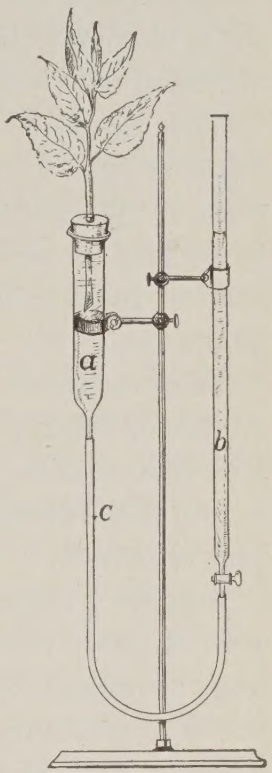


FIG. 14. — Burette potometer for quantitative measurement of water absorbed by a transpiring branch. The burette can be replaced by a pipette, with still more rapid readings. *a*. Glass tube to hold the transpiring branch. *b*. Measuring burette. *c*. Rubber tubing, which must be completely filled with water. Avoid air bubbles.

Index of transpiring power. — Many years ago Stahl used filter paper impregnated with cobalt chloride solution to demonstrate transpiration. When the paper is dry, it is bright blue in color, but in a moist air it turns pale blue and then pink. It undergoes the same color changes when held against the surface of a leaf under glass or mica plates. The length of time required for the change from blue to pink may be used as a rough measure of the rate of water loss from the leaves. Thus in the *Catalpa* leaf, which is hypostomatous, that is, has its stomata only on the under surface, it may require three or four minutes for the paper to change from blue to pink on the under side of the leaf; but it may require more than half an hour for the same amount of change on the upper surface, where there are no stomata.

During recent years the manufacture of cobalt chloride paper has been standardized, and the methods of use also have been very carefully standardized, until it is possible now to use it as an accurate quantitative measure of the transpiring power of the leaf.[1] Some standard of comparison had to be chosen. Permanent color standards have been developed so that a definite amount of color change in the cobalt paper can be used for each determination. In addition, it was necessary to have some standard evaporating surface with which to compare the leaves. For this standard evaporating surface it is now

[1] Bakke, A. L. Studies on the transpiring power of plants as indicated by the method of standardized hygrometric paper. *Jour. Ecol.* **2** : 145–173. 1914.

Livingston, B. E., and Shreve, Edith B. Improvements in the method for determining the transpiring power of plant surfaces by hygrometric paper. *Plant World* **19** : 287–309. 1916.

customary to use saturated blotting paper, or saturated porous porcelain, which has the same evaporation power as pure water.

The cobalt paper is exposed over this surface at a distance of 1 mm., under a glass cover. The number of seconds required for a standard piece of cobalt chloride paper to change from standard bright blue to standard pale blue when so exposed, serves as the basis of comparison for the leaves of plants. The value assigned to this index is unity. Suppose that it requires 15 seconds for this change in color to take place in the standard instrument. Then if a leaf be tested, and found to require 30 seconds, its transpiring power is only half as great as that of pure water. The index of its transpiring power is 0.5, or 50 per cent.

These methods have made possible many interesting and valuable studies of different species of plants in the same habitats, and the same species in different habitats. They also give to our knowledge and to our methods of experimentation along these lines an exactness which is very desirable.

Relative transpiration. — The transpiration of water from a definite area of plant surface may be compared to the evaporation of water from an equal area of some atmometer surface. The ratio of transpiration to evaporation, T/E, in this case is called the relative transpiration. The value of this ratio varies from hour to hour during the day, and with all the varying conditions of life which may affect one factor of the ratio more than the other. The value of E is determined by such factors as the air temperature, relative humidity, illumination, and wind velocity. These factors also influence transpiration, but usually to a different degree than they affect evaporation, for the plant may regulate its transpiration to a certain extent, particularly when the stomata are partially closed.[1] This regulation may be exercised through the opening and closing of stomata, by suffering incipient drying of its internal surfaces,[2] by developing strongly hydrated colloidal material in its cells, or by changes in the permeability of its protoplasmic and protecting membranes.

The study of relative transpiration of plants under different combinations of environmental conditions is interesting, and provides a

[1] Loftfield, J. V. G. The behavior of stomata. *Carnegie Inst. Publ.* No. 314. Washington. 1921.

[2] Livingston, B. E., and Brown, W. H. Relation of the daily march of transpiration to variations in the water content of foliage leaves. *Bot. Gaz.* **53**: 309–330. 1912.

———. Incipient drying in plants. *Science* **35**: 394–395. 1912.

rough measure of the response of plants to those factors which cause loss of water.

Stomata. — The guard cells of the stomata are different from the rest of the epidermal cells in form, in the peculiar unequal thickening of their walls, and generally in the possession of chloroplasts. These characters and the position of the guard cells with reference to the adjacent subsidiary cells determine simultaneous differences in turgor and make them behave differently from the others. In general when turgid, they become arcuate, and when flaccid, they straighten. The mechanics of these movements differs considerably with differences of form, structure, and position, and in none of the several types that have been distinguished is it fully understood.

It seems evident, however, that the changes are related to turgor changes in the guard cells. Two theories have been proposed to account for these changes in turgor, a theory of carbohydrate transformation, and a theory of colloidal hydration and dehydration.

The first of these theories explains the changes of guard cell turgor in terms of transformation of starch to sugar and sugar to starch again during opening and closing. It has been observed that during illumination, the guard cells are practically free of insoluble carbohydrates like starch, but contain much soluble sugar which of course causes osmotic inflow of water, and high turgor pressure in the guard cells. The high pressure causes the cells to change shape, due to construction of the walls of the guard cells, so that the slit between them, the stoma, is opened. When darkness ensues, these soluble sugars are usually condensed back into starch, which, because of its insolubility, has no osmotic effects. The water that has been present in the cells now diffuses into the surrounding cells, the turgor falls, and the guard cells close. On reillumination once more the starch becomes sugar, and the high pressure is reëstablished. This theory is based upon the observed periodic appearance and disappearance of starch from the guard cells, and the corresponding decrease and increase of osmotic concentration in the guard cells as determined by the plasmolytic method. Iljin[1] claimed to have observed changes in osmotic concentration in the guard cells of as much as 80 atmospheres between the open and closed condition. Others have found smaller values.[2]

[1] Iljin, W. S. Die Regulierung der Spaltöffnungen im Zusammenhang mit der Veränderung des osmotischen Druckes. *Beih. bot. Centralbl.* **32** : 15–35. 1914.

[2] Wiggans, R. G. Variations in the osmotic concentration of the guard cells during the opening and closing of stomata. *Amer. Jour. Bot.* **8** : 30–40. 1921.

Recently, the hydrogen ion concentration has been found to be important in the opening and closing of the stomata. Sayre believes that the acidity merely controls the hydrolysis and condensation of the carbohydrates, certain degrees of active acidity favoring hydrolysis, and others the condensing action of the diastase system.[1] The mechanism would still be a carbohydrate mechanism in which the nature of the change is determined by the reaction of the cell contents.

It has been observed, however, that stomata can open and close very quickly, too quickly, possibly, for such a mechanism to operate. Moreover, stomata have been seen to open and close without apparently containing any visible starch. And they can open in a few minutes, without any very evident change in the amount of starch present in the guard cells. These observations make the validity of the carbohydrate theory questionable as a complete explanation of stomatal opening and closing.

A different interpretation has been proposed by Scarth,[2] who believes that certain colloidal protein-like materials in the guard cells become greatly swollen at certain hydrogen ion concentrations, and dehydrate rapidly at other degrees of acidity. The highly hydrated colloids may exert sufficient pressure in the guard cells to cause their opening. During the day the contents of the guard cells are alkaline due to the fact that the CO_2 is being used for photosynthesis by the chloroplasts in the guard cells. In this condition the colloids swell very strongly, and the guard cells are open. But when, on account of darkness or low light intensity, the photosynthesis stops, then carbon dioxide of respiration accumulates in the guard cells, they become more acid, the colloids lose their bound water, or become dehydrated, the water diffuses out of the guard cells into the surrounding cells, and the guard cells close from loss of turgor. If the products of respiration become too abundant, hyperacidity may develop and cause the colloidal material to become swollen on account of excess acid. It is well known that protein colloids swell in both basic and acid media, but remain unswollen or much less swollen at the isoelectric point, the point where the proteins are essentially un-ionized. Hyperacidity might develop during long periods of darkness, and this may explain why some stomata open at

[1] Sayre, J. D. Physiology of stomata of *Rumex patientia*. *Ohio Jour. Sci.* **26**: 233–266. 1926.

[2] Scarth, G. W. The influence of H-ion concentration on the turgor and movement of plant cells with special reference to stomatal behavior. *Proceedings of International Congress of Plant Sciences*. Ithaca. vol. II. 1151–1162. 1929.

night, as has been observed by Loftfield and others. When the cells are once more illuminated, they again use up the accumulated CO_2, become alkaline, colloids swell, and the stomata open. This behavior of the vacuolar colloids of the guard cells has been photographed, and is striking evidence in support of this theory.

Since alkaline conditions are known to favor starch hydrolysis, this would account for the fact that, a couple of hours after illumination, all of the starch of the guard cells is hydrolyzed. But it would seem to be more an after-effect than the main cause of the stomatal changes. Careful study of the behavior of stomata in a number of representative plants should enable us to decide which of these two views is correct. The movement of guard cells may well be the result of changes in both the colloids and the starch and sugar. But the colloidal changes seem to occur more swiftly than the hydrolysis and condensation of carbohydrate. The latter chemical change may be only a subsidiary part of the mechanism.

The longitudinal thickenings are elastic and are supposed to straighten the cells when they become flaccid. The auxiliary cells are supposed to offer proper bracing for the guard cells so that turgor will arch them.

Regulation by stomata. — Naturally the guard cells are most likely to be turgid when the water supply is good; then the opening of the slit between them permits free diffusion of the water vapor into the outer air. Conversely, the guard cells become flaccid with scant water, straighten elastically, and practically close the slit. This sort of adjustment exercises a certain amount of control over water loss; but as has been indicated, the main factor in the opening and closing of stomata is light.

There are several types of stomatal behavior. Some plants, especially bog plants, have their stomata open most of the time, at night as well as during the day. Among our cultivated plants, the potato also keeps its stomata open at night.

The cereals, like barley, have their stomata closed all night, and only partially opened even during the day. They very rarely open more than 10 to 20 per cent of their full size.

The common thin-leaved plants, like alfalfa, sunflowers, mustards, and the great majority of dicotyledonous mesophytes, have their stomata open in the daytime and closed at night.

It was at one time thought that stomatal closure had no real regu-

latory value with reference to water loss. Certain studies seem to show that the closure occurred only after wilting had taken place. But more recent investigations have shown that mesophytic plants may retain their water better than xerophytic plants when both are placed under the same conditions of high transpiration. Apparently as long as the stomata are wide open, the rate of water loss is dependent on the physical environmental conditions. But when the stomata are more than half way closed, they begin to exercise some control over the rate of water exit; and the more nearly closed they are, the more perfect this control becomes.[1]

In many ways, however, it is better to think of transpiration in terms of energy loss rather than in terms of water loss. The reason for this has been stated in an earlier paragraph. The stomata of ordinary plants open in the morning when energy receipt begins, and at night, when energy receipt ceases, or is at a minimum, they close. In this way stomatal opening and closing seem to be related to the problems of dispersal of excess energy. It must be remembered, of course, that some plants have immobile guard cells, or guard cells that respond very sluggishly to external stimuli. In many instances where the need of an effective mechanism seems to us most obvious, the stomata are found to be inefficient regulators. They should not be looked upon as having the power of exact adjustment of the plant to its environment, but as exercising some control, along with other factors like incipient drying of internal surfaces.

Factors in transpiration. — The amount of water lost from a given surface of plant tissue is extremely variable. The humidity of the air, its temperature and pressure, which also affect humidity, the velocity of the wind, and the temperature of the plant are the chief factors which cause the rate of evaporation to vary. The simplest mode of determining evaporation quantitatively is by weighing potted plants at intervals, having prevented evaporation from the surface of pot and soil by some impervious covering of rubber, metal, or wax. It is not justifiable, however, to apply these data to plants in nature.

Humidity. — In a saturated atmosphere there can be no water loss. Yet experimentally this is very difficult to establish. The reason is to be sought in two directions. First, it has been found practically impossible to maintain an atmosphere absolutely saturated at all times,

[1] Loftfield, J. V. G. The behavior of stomata. *Carnegie Inst. Pub.* No. 314. Washington. 1921.

for that means an invariable temperature, which, under other conditions necessary to the experiment, is unattainable. Second, even were the proper external conditions attained, the plant by respiration would be a little warmer than the air, and the air next the plant, therefore, would not be quite saturated; so some small amount of evaporation might take place. Yet during rain, mist, or fog, practically no evaporation occurs; and as the humidity decreases from 100 per cent to the 70 per cent of a moderate day or to the 50 per cent of a dry day, evaporation increases. As the humidity fluctuates from day to day or even from hour to hour, the evaporation varies likewise. The most marked changes in relative humidity are due to the rising or falling temperature of the air. As temperature rises, relative humidity becomes less, the heat energy imparted to the plant is greater, and evaporation is increased by both causes.

Barometric pressure. — As the air pressure is reduced the boiling point of water falls; so fluctuations in the barometer indicate inverse changes in the rate of transpiration. Yet these variations at any locality are insignificant; the reduction in air pressure becomes important only in comparing plants at high and low altitudes. In alpine regions, where low barometer may coincide with low humidity and therefore intense light, the excessive evaporation often becomes a powerful factor in dwarfing plants and in controlling their distribution.

Temperature. — The temperature of the plant itself tends normally to equal that of the air, since its extended surface permits quick gain or loss of heat toward equilibrium. A rise of temperature in the air, therefore, is quickly followed by a rise of temperature in the plant, and (even with no change in the relative humidity of the air) by increased transpiration. But the temperature of the plant depends also upon the energy absorbed by the green pigment in diffuse light or direct sunlight. In diffuse light the greater part of this energy is used in food making, and only a small portion exerts a heating effect. But in sunlight two thirds to three fourths of that absorbed is free to heat the tissues, and as soon as that begins, evaporation is thereby much accelerated. This tends to dissipate the heat.

It has been proposed to call the evaporation due to the excess of energy absorbed by the chlorophyll, *chlorovaporization*. The term has its only value in promoting recognition of the fact; but chlorovaporization cannot be distinguished practically from the rest.

Wind velocity. — The velocity of air flow modifies the rate of transpiration mainly by removing moist air from the neighborhood of the leaf, and so shortening the path of diffusion for the water molecules. In still air there is a tendency for the water vapor to remain near the stomatal openings, and to form what have been called equidensity vapor shells over them.[1] The accumulating water vapor diffuses outward from the stoma in every direction, and the vapor density decreases as the distance from the stoma increases. When the air is moving with sufficient velocity, these more nearly saturated portions of the atmosphere are swept away, bringing drier air into direct contact with the leaves. This increases the gradient of diffusion, by decreasing the distance the water molecules must travel.

Amount transpired. — Because of the extreme variation, from zero to the maximum, a quantitative statement of the amount of transpiration is of little value, though a voluminous literature records an enormous number of observations and calculations. The following will serve as illustrative examples.

MEASURED EVAPORATION FROM 100 SQ. CM. OF LEAVES (200 SQ. CM. OF SURFACE) IN BRIGHT DIFFUSE LIGHT, AT ABOUT 20° C., WITH HUMIDITY ABOUT 50 PER CENT

	1 hr.	24 hr.
Phaseolus vulgaris	0.117 gm.	2.81 gm.
Hedera Helix	0.17	4.09
Begonia argentea	0.19	4.57
Coleus Blumei	0.211	5.06
Cucurbita Pepo	0.224	5.39
Ficus elastica	0.262	6.3
Helianthus annuus	0.5	12.0
Lupinus albus	0.594	14.27
Chrysanthemum frutescens	0.681	16.35
Vicia Faba	0.683	16.4

Hemp plants in a season of 140 days were estimated to evaporate (each) 27 kg. and sunflowers 66 kg. of water. It is estimated that if the water evaporated by the following cereals was again condensed on the area occupied by each sort, say 1 sq. m., it would cover the ground in the case of rye to a depth of 83 mm., wheat, 118 mm., and oats, 127 mm. The average annual rainfall in the north central states is in the neighborhood of 1000 mm., so that one twelfth to one eighth of the total passes through such cereals.

A birch tree with 200,000 leaves is estimated to evaporate on a hot day 300 to 400 kg. A beech, 15 years old, is said to average about 75 kg. per day in the months

[1] Renner, O. Beiträge zur Physik der Transpiration. *Flora* **100** : 451–547. 1910.

from June to September, inclusive. At that rate a hectare of beech forest containing 400–600 trees would evaporate some 20,000 barrels. In all these calculations and estimates a liberal allowance must be made for errors.

Water requirement. — The amount of water loss bears a rough relationship to the amount of dry weight of tissue the plant can produce. The water requirement may be defined as the number of pounds (or grams) of water required by the plant for the growing of one pound (or gram) of dry matter.[1] The water requirement would vary, of course, with the conditions of the environment. Any factor retarding growth, without equally retarding use of water, would increase the water requirement. Similarly, any factor increasing growth, without equally increasing the use of water, would depress the water requirement. Every factor of soil and climate would help to determine the exact ratio of water to growth in each individual case. There are also internal factors which modify the water requirement of plants. There is no definite water requirement for each kind of plant, but in a rough way one can determine that some plants use water economically and that others are extravagant in their use of water.

In the case of sorghums, the water requirement is about 250; that is, a unit of dry weight growth increase is accompanied by the utilization of 250 units weight of water, approximately. Corn has a requirement of 300 to 350, and many of our crop plants, like oats, potatoes, wheat, etc., use from 400 to 500 times as much water as their dry weight growth. Alfalfa is extravagant in its use of water, requiring 800 to 1000 times as much water as dry weight produced. The sorghums are fairly good dry land plants and one reason for their success in a dry habitat is their economical use of water. Alfalfa, although it is extravagant in use of water, roots so deeply that it does very well in the great plains region where water is not plentiful.

Reduction of water loss. — Among all the agencies that affect the form and mode of development of plants none has more influence than water, and the relation between the available supply and the loss by evaporation. In the peculiarities of form and structure which seem related particularly to water, many see "adaptations" to a habitat with much water, a moderate amount, or a scanty supply. Thus the

[1] Briggs, L. J., and Shantz, H. L. The water requirements of plants. *U. S. Dept. Agr. Bureau Plant Ind.* Bulls. **284, 285.** 1913.

Shantz, H. L., and Piemeisel, Lydia N. The water requirement of plants at Akron, Colorado. *Jour. Agr. Res.* **34**: 1093–1190. 1927.

cutinization of the epidermis, the formation of a waxy or resinous coating, and the development of cork are structures which reduce the loss of water. In other plants the scanty or fleshy foliage, the complete absence of leaves, the development of water-holding tissues, the short cylindric or globular fleshy body, the deep-running roots, and many other peculiarities (treated more fully in Volume III, *Ecology*) are considered as " adaptations " to a dry climate. It would be better to look upon them as effects of climate and similar factors, since experiments indicate that such " adaptations " can be produced at will, even in one generation, by cultivation under appropriate conditions.

2. EXUDATION OF WATER

Forms of exudation. — Besides the vapor which constantly exhales from plants, liquid water exudes from certain regions intermittently. The places whence it issues are, first, certain specially permeable areas of the permeable regions in an uninjured plant; second, the conducting tissue when opened by some wound. *Guttation* is the escape of water in drops from uninjured plants. It occurs especially in leaves in the vicinity of the tips of main veins, where there are stomata, often enlarged, called water pores, through which water exudes. *Bleeding* is the oozing of water from the water-conducting tissues when ruptured. It is especially notable in the spring, before the foliage is fully developed. *Secretion* consists in the exudation of water and solutes from certain specialized cells, constituting a gland, and found on various parts of plants, but especially on foliage and flower leaves. All these processes are essentially similar, with minor differences.

Guttation. — Guttation may be readily observed by inverting a glass jar over grass seedlings growing in well-watered soil and thus checking the evaporation. The coleoptile of Avena is especially fine for demonstrating this phenomenon, as it shows exudation in a few minutes. In a short time a water drop accumulates at the tip of the blade and enlarges until it runs down or falls off. Leaves of vigorous plants of many species (*e.g.* aroids, fuchsia, cabbage, nasturtium) under like conditions show droplets of water at the tips, or at marginal teeth, or near the end of main ribs.

Accessory structures. — In all these cases an examination shows essentially the same features: (*a*) a rift in the epidermis, or one or more water pores, over (*b*) a rather large chamber, which is bounded by (*c*) more or less specialized colorless parenchyma cells (*epithem*), and

near by (*d*) the tracheids at the end of a vein. The rift in the epidermis may be due (as in grasses) to growth and consequent stretching and rupture. The water pore is simply a deformed stomatal apparatus whose dilated slit is always wide open because the distorted guard cells are no longer motile. When the water pore is single, it is usually greatly enlarged and deformed; when there are a number together, each is more nearly like an ordinary wide-open stoma. The cells lining the substomatal chamber differ from the mesophyll cells chiefly in lacking chloroplasts. They resemble the sheath of colorless cells, the so-called transfusion tissue, that adjoins the tracheids, which form the endings of the water-conducting bundles of the leaves. In some cases this epithem seems to be a water-secreting tissue and to deserve the name water gland; in others it seems to be passive and removal of the epithem by amputation does not always stop the exudation.

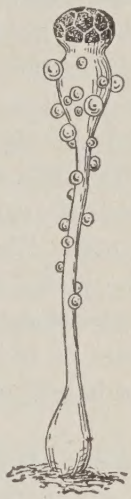


FIG. 15. — Sporangiophore of *Pilobolus*, showing exuded water. — Adapted from ZOPF.

Guttation in fungi. — Guttation is not confined to the higher plants, nor are there always such elaborate accessory structures. It occurs in its simplest form in many fungi. Thus *Pilobolus crystallinus* owes its specific name to the droplets of water which appear on its sporangiophores (fig. 15), and *Merulius lacrymans*, the dry-rot fungus, likewise, "weeps" so much water that it accumulates in big drops on the surface of its sheet-like mycelium.

Nightly guttation. — In nature the checking of evaporation, which results in guttation, occurs chiefly at night, when many young plants exude water. What remains adherent at the water pore may be partly resorbed when transpiration begins.

This seems to be the way in which a destructive bacterial disease of cabbage (black rot) infects the plants. By contamination of the hanging drop the bacteria find their way into the chamber as the drop evaporates or is resorbed, there develop and so kill the adjacent cells, whence they enter the xylem bundles and work backward, killing and rotting the bundles. When the crop is gathered and stored, they develop further, until the head is spoiled by the extension of the blackened and rotted tracts in the blanched leaves.

One may easily observe the exudation of water from the leaves of lawn grasses early in the evening, when the "dew" is said to be "fall-

ing." The warm soil conduces to the entry of water; the cooler air checks evaporation; these conditions permit maximum turgor; guttation at the tips of uninjured leaves, or, more often and more promptly, bleeding from the cut ends of the leaves is the result. This shows that the epithem is not necessary to the phenomena of guttation in ordinary grasses. Dew, of course, may form under proper conditions; but exuded water forms a great part of what passes as dew.

Artificial guttation. — Guttation may be produced artificially by injecting water under pressure into the stem of a plant known to have water pores, as by attaching the end of a cut shoot to a water tap. Presently droplets exude at the usual places. It is usually assumed that the water is thereby forced through the plant tissues, but as city water pressure varies from 2–3 atmospheres (seldom more, and less will often answer), it is doubtful if so low a pressure (as compared with the 3–10 atmospheres of common turgor pressure) would be adequate to do this (see further, p. 80).

Quantity exuded. — In a few plants, especially in aroids, guttation under favorable conditions is so rapid that water drips from leaf tips or is even ejected. Thus a vigorous leaf of *Colocasia* has yielded 1008 cc. of water in 9 days, the water dropping at the rate of 85–100 drops per minute at times. *C. nymphaeoides* has been observed to eject a stream of minute droplets (at a rate of 195 per minute, so that it seemed almost a continuous jet of water) to a height of about 1 cm.

Advantage? — Seeing the structural features which permit guttation, one naturally asks, Is it advantageous? To that question no certain answer can be given. It is assumed that the free escape of water at these points prevents its escape elsewhere, and therefore prevents the infiltration of the aërating system with water, which would greatly retard the entry of gases and so the manufacture of food. But there are so many plants which lack the arrangement for guttation that one must doubt if this answer be adequate.

Bleeding. — Bleeding may be observed when vines are pruned rather late, or in many cases when a potted plant is decapitated. It must be distinguished from exudation due to heating the water and especially the gases contained in the woody parts of a plant, which has the same general effect. Thus, when a green stick is put on the fire, the scanty sap presently boils out of the ends; for the expansion of the gases and of the water, and later the steam generated by the fire, drive it out forcibly. Or if on a cold day in winter, one bring into a warm room a branch of a shrub or tree, water will soon ooze out at the cut surface. Here the gases in the wood are warmed (for though fuller of water in

winter than at other times, the wood is never free from gases, else no green wood would float); they expand, and press upon the free water, forcing it out at the nearest opening. True bleeding, however, is restricted to live plants and is quite independent of any gas pressure due to heat.

Industrial applications. — Collecting maple sap for sugar or sirup making is partly an industrial application of bleeding. The work is often begun when only the heating of the twigs on a warm sunny day is active in forcing out the water through the wound made in the trunk; but a great part of the later exudation is dependent on other causes and must be accounted to this extent as true bleeding. Another commercial application of bleeding is found in the collection of the sap of various species of *Agave* in Mexico and Central America for the manufacture of fermented and distilled liquors. The process begins with cutting out the huge bud at the time when the plant, at the end of 5–15 years' growth, is about to send up the great flower stalk, 12–20 cm. in diameter and 6–10 m. high. Into the basin formed by removing the bud, the plant exudes several liters of water a day, for two months or more; this is collected daily, and after the addition of milk and fermentation is esteemed as a beverage, called *pulque*. Extensive plantations are devoted to raising the agave or maguey, and pulque trains run into the large cities, as milk trains do in this country. The fermented sap is also distilled to make various fiery alcoholic drinks.

Conditions. — The conditions under which bleeding occurs are like those for guttation, a liberal water supply and limited transpiration; that is, the conditions which permit maximum turgor. Even so, not all plants bleed; hence it cannot be at all necessary, nor can the causes be universally active.

Cause of exudation. — The cause of bleeding and guttation is to be sought in the development of high turgor in certain cells (on account of the osmotic pressure of the solutes in them to which the protoplast is impermeable), which is made possible by adequate water supply. To stop evaporation by making the air about the aërial parts very moist, or by cutting away the aërial parts, or to have limited evaporation because the foliage is not yet fully developed, are merely ways by which a water supply, that might otherwise be barely enough to cover the evaporation, is made ample; and this permits high turgor when other conditions are met. When the turgor rises to a certain point in the active cells, it seems that water is exuded.

This may be mere filtration under pressure. But we may also conceive it to be due to a sudden alteration of the permeability of the cytoplasm, wrought by the very pressure itself. In that event, upon the relief of pressure when

the outgo occurs, there would be a gradual recovery of impermeability and consequently of turgor to the maximum; then another automatic change of permeability, a consequent outrush of water, and so on.

This outflow naturally cannot be pure water;[1] but on the theory of filtration the water will contain at least the substances to which the protoplast is permeable; and on the second hypothesis, any or all solutes might be released, the sap as a whole escaping. In the water there are often substances in small amount, regarding whose osmotic relations we are ignorant, though the general assumption is that they could not pass the cytoplasm without some special modification of its permeability. When that is demonstrated, it will be necessary to adopt the second hypothesis, which is also used to account for the presence of such substances in secretions (see p. 84). Until then it will suffice to assume that they issue with the water because they are free to do so.

Tissues concerned. — In the case of *Pilobolus* and like plants, the turgor which causes the escape of water evidently arises in the very cell or coenocyte from which it escapes. This may also be the case in guttation among seed plants. The epithem of the water chamber, receiving an adequate supply of water from the adjacent vein, may develop turgor sufficient to cause water to pass the cytoplasm and the wall. It is obvious that to issue from the free surface it will encounter less resistance than elsewhere; consequently it takes this direction. The chamber fills and water soon oozes from the water pore. But the epithem cannot develop an adequate turgor unless the water supply is sufficient. That may be made sufficient either by checking the transpiration, or by forcing water up to these cells so that they may get enough, even though transpiration is unchanged. Water may be supplied thus artificially by cutting the stem and attaching it to a water tap; or the same end would be accomplished in nature if the root cortex had a supply adequate to enable it to become fully turgid and exude water under pressure into the conducting system.

Root pressure. — The condition just mentioned no doubt often exists in the roots of plants, and probably is the cause of exudation of liquid water from decapitated stems which exhibit bleeding. Al-

[1] Wormall, A. The constituents of the sap of the vine (*Vitis vinifera* L.). *Biochem. Jour.* **18**: 1187–1202. 1924.

Priestley, J. H., and Wormall, A. Solutes exuded by root pressure from vines. *New Phytol.* **24**: 24–38. 1925.

though the name root pressure has been given to this phenomenon, it must not be forgotten that similar turgor pressure may be developed by thin-walled living cells anywhere in the plant body. In certain glandular hairs, turgidity of the row of cells forming the hair gives rise to a unilateral exudation of liquid from the glandular apical cell. The cells of the root cortex which lie between the root hair and the parenchyma cells which border the tracheae may by turgor pressure cause exudation of water into the tracheae on the same principle as that of the glandular hairs just mentioned. Such unidirectional water movement is not easily explained. Electrical conditions existing in the membranes may sometimes favor the transfer of water in one direction rather than in another; or one might imagine that in some way the tracheae came to have more concentrated sap than the bordering living cells, and osmotic action then caused the exudation and bleeding. In some plants the endodermis of the root has been found to have the characteristics of a semipermeable membrane, even the walls sharing this property with the living protoplasm. It may form the basis, at least, of a group of living cells which act together like a single semipermeable membrane, within which this exudation pressure, or turgor pressure, of bleeding is developed.[1]

During the period of most rapid transpiration in midsummer, root pressure is negligible, and the water may be drawn into the tracheae under the negative pressure of the cohering water columns in the tracheal system.[2] If this negative pressure, caused by water deficit in the leaves above, is greater than the turgor pressure of the root cells, it would be able to cause exudation of water into the tracheae by a sort of suction upon the root cells, which would then attempt to replace the water by absorbing from the soil.

Amount and pressure. — Experiments on bleeding are often conducted with potted plants, which are decapitated, and to the stump is affixed apparatus for measuring the amount of water exuded, or the pressure with which it is forced out. With trees, the trunk is bored and the receptacles or gauges attached. A few examples will give an idea of the maximum quantity of the sap and the pressures involved.

[1] Priestley, J. H. The mechanism of root pressure. *New Phytol.* **19** : 189–200. 1920. Overton, J. B. The mechanism of root pressure and its relation to sap flow. *Amer. Jour. Bot.* **8** : 369–374. 1921.

[2] Shull, Charles A. Imbibition in relation to absorption and transportation of water in plants. *Ecology* **5** : 230–240. 1924.

A calla lily bled 39 cc. in 24 hours. A vigorous European grape sometimes exudes nearly a liter per day. The Mexican agaves, cultivated for this purpose, are said to give out 5–6 liters daily for several months. Under favorable conditions, the sugar maple yields 5–8 liters in the course of a day, and the birches give out about as much.

The pressures, recorded in millimeters of mercury (760 = 1 atmosphere), vary from 0 to

Ribes rubrum (red currant)	358
Acer platanoides (sycamore maple)	347
Acer saccharum (sugar maple)	1033
Psedera quinquefolia (Virginia creeper)	615
Betula alba (white birch)	1390
Betula lutea (yellow birch)	1815
Betula lenta (black birch)	2040
Vitis vinifera (European grape)	860

Much study has been given to variations in the amount and pressure of bleeding; seasonal and possibly diurnal fluctuations have been discovered; but inasmuch as turgor pressure must be influenced by transpiration, itself of infinite variability, the precise results of these studies are not important.

The limited movement of water through submersed aquatics cannot be due to transpiration, and is probably not a case of guttation. The experimental evidence is scanty and the movement may be referable to the larger heating effects on the leaves as compared with the stems. This should create a slow movement of water out of the leaf, to be supplied from below.

FIG. 16. — Young glandular hair of *Pelargonium*: *c*, cuticle; *o*, volatile oil.

Secretion. — Secretion is a much more general and varied phenomenon than guttation or bleeding. It is performed by more limited and specialized tissues, called glands, and the variety of substances which escape is much greater, though the amounts lost are much smaller. Many of the secretions are of such a nature that they play an important part in the life of the plant; others are of no use so far as we know and are therefore called waste products. No distinction can be made in plants between useful secretions and waste excretions.

Glands. — There are some glands which secrete water, with no distinctive solutes, like that which escapes in guttation and bleeding; and because there are no distinctive solutes these are called water glands. Glands are named usually according to the most abundant or character-

istic material they secrete. Thus those in whose secretion calcium salts become conspicuous by concentration are called lime glands; digestive glands secrete water containing enzymes. Most common of all are the nectar glands of nectaries, abundant in flowers, but found also on other parts as extra-floral nectaries whose water is sweet with sugar and often fragrant. Not all glands, however, secrete water and its solutes. There are glands whose secretion is an essential oil,[1] of which a great variety are formed. Still others secrete resin, which may be formed from an essential oil.

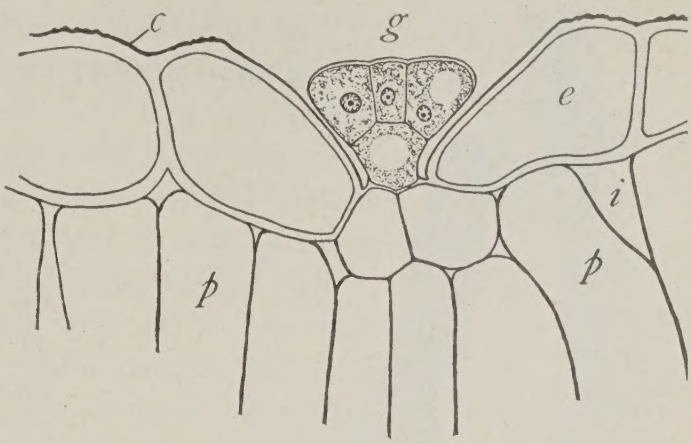


FIG. 17. — Gland (*g*) from the upper surface of the leaf of lilac (*Syringa vugaris*): *e*, epidermis; *c*, cuticle; *p*, *p*, palisade cells; *i*, intercellular space

Forms of glands. — The form of glands is various. A single epidermal cell may differ from its neighbors; it may be level with them, or sunk, or raised upon a shorter or longer stalk, like the glandular hairs (fig. 16). A filament or a cluster of such cells may form a stalked gland (fig. 17); the gland cells may form a rather indefinite mass, or they may line a shallow cavity (fig. 19), or a deep pouch, as in the nectary of the nasturtium (fig. 18); or they may be the epithelium of a simple or branched duct, as in the lilies (fig. 20). Nor do all glands pour out their secretion on the surface. The gland cells may part when young, forming intercellular spaces into which the secretion exudes to escape through water pores. Or a single intercellular space may develop in the center of the group (fig. 21) which receives the

FIG. 18. — Flower of nasturtium (*Tropaeolum majus*) cut through the middle to show the spur (*s*) and the nectar (*n*).

[1] Not true oils, from which they may be distinguished by making only a transient grease spot on paper.

secretion; then as the gland and space grow, the secreting cells form an epithelium for a closed reservoir, larger or smaller, containing the secretion. Or, later, by the destruction of the gland cells loaded with the secretion, it finally occupies their place as well as the

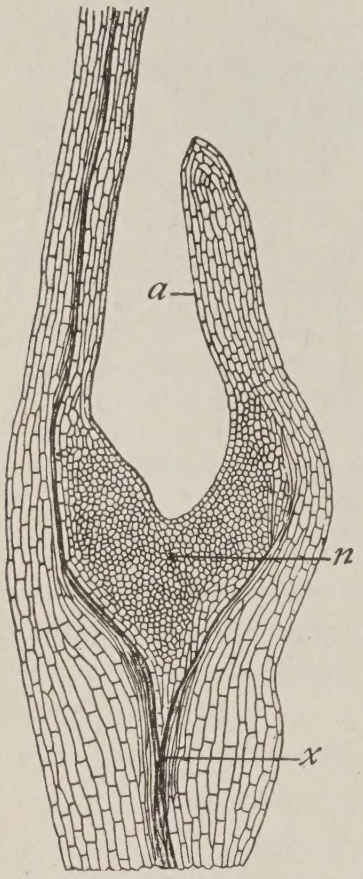


FIG. 19. — Section through a petal of buttercup (*Ranunculus*), showing nectar gland (*n*) and shallow receptacle formed by the "nectary" (*a*). Note bundle of conducting tissues (*x*). — After BONNIER.

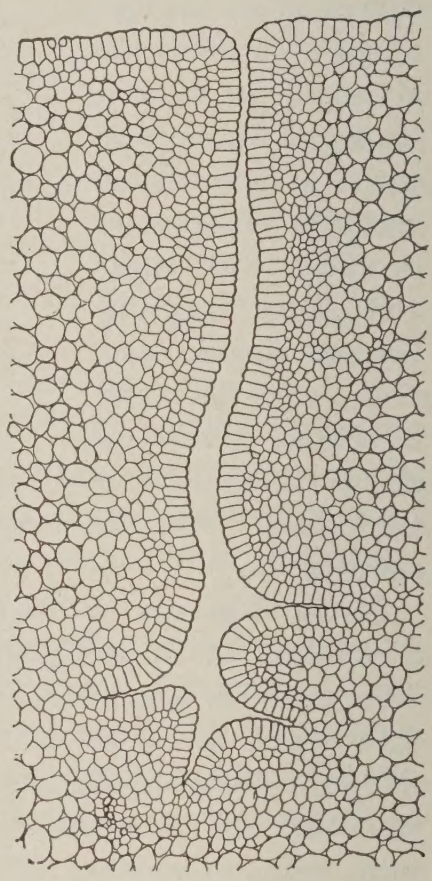


FIG. 20. — Nectar gland in the ovary of day lily (*Hemerocallis flava*). — After SCHNIEWIND-THIES.

intercellular space, and reaches the surface only by mechanical rupture of enveloping tissue (fig. 22).

Emission of secretions. — Very little is known of the chemical processes by which the peculiar materials of the secretion are formed. Each sort of gland doubtless pursues a different course. Nor is it possible to account for the emission of the various substances. Some, like cane sugar, are known to be retained ordinarly by the cytoplasm; yet nectar glands secrete sugar one or more times. Others, for example, enzymes, have a composition which, though imperfectly known, is such as to suggest that the cytoplasm would usually be im-

permeable to them; yet digestion occurs in such places as to make it certain that enzymes are able to pass out of the cells in which they arise.

The problem, therefore, is: How can solutes pass the ectoplast usually impermeable to them? The answer is merely in the form of a hypothesis, like the one already proposed to account for guttation and bleeding. If the accumulation of the solute causes a rise of turgor, it is conceivable that the very pressure itself might work such a change in the cytoplasmic membranes that they alter their permeability and permit the outrush of water and its solutes in the direction of least resistance, which will be toward the free surface. Whether a renewed secretion will take place depends on the further activity of the cell. Given a repeated formation of the secretion, it might escape again. The hypothesis then suggests a rhythmic variation in the permeability of the cell membranes, the secretion being formed inside the cell.

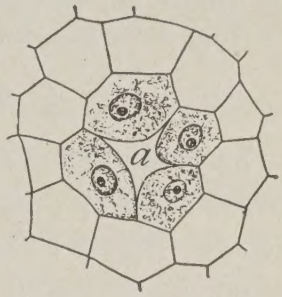


FIG. 21. — Young resin gland of fir (*Abies*): *a*, duct, an intercellular space formed by the separation of the four nucleate cells. — After TSCHIRCH.

This hypothesis is clearly inapplicable to secretions which are not miscible with water, like essential oils and resins. They are possibly formed, however, in the very wall itself, and thus the material may not have to traverse the ectoplast as resin or oil. Unfortunately, even the place of their origin is still obscure. In resin ducts the resin is probably formed by the protoplasm of the epithelial cells surrounding the duct. Droplets of resin appear between the protoplasm and wall only on the sides of the cells bordering the ducts. Turgor pressure may assist in forcing the resin through the walls into the ducts.[1]

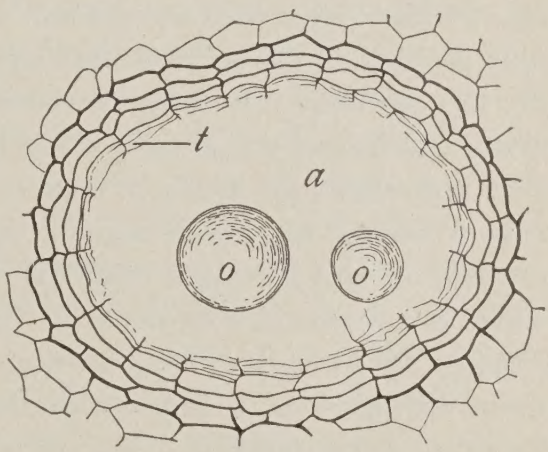


FIG. 22. — Oil receptacle (*a*) in orange (*Citrus Aurantium*), formed partly by splitting, but chiefly by destruction of secreting cells and their neighbors (*t*); *o*, *o*, drops of essential oil. — After TSCHIRCH.

Rôle of certain secretions. — Nectar is gathered by many insects, some of which store it, after partial digestion, as honey. While the floral glands are being explored for nectar, the visitors become dusted with pollen and transfer this to ripe stigmas of the same or other flowers, thus in-

[1] Hannig, E. Untersuchungen über die Harzbildung in Koniferen Nadeln. *Zeitschr. Bot.* **14**: 385–421. 1922.

suring pollination in many cases where otherwise it might not occur (see vol. III on pollination). The rôle of extra-floral nectar is not clear. Digestive glands, most definite in insectivorous plants (p. 157), secrete enzymes (p. 173) by which the soft parts of captured insects are dissolved. Essential oils (p. 197) sometimes prevent plants from being eaten by animals.

3. THE MOVEMENT OF WATER

Transpiration stream. — In the two foregoing sections it has appeared clearly that the region where water enters a plant and the region whence it leaves are rarely identical, but that these parts are more or less widely separated. There must be, therefore, movement of water through the body. Small quantities of water are used in the body for saturating new-made materials and parts, and for food making by green plants. Somewhat larger quantities are exuded by guttation, bleeding, or secretion. But the dominant cause of movement is to be found in evaporation, for the amount thus leaving the body is often many times greater than all other quantities combined. So considerable is it that the flow through the body is figuratively known as the transpiration stream.

This transpiration stream is a rather constant feature of plant life, for the aërial parts of the plant are nearly always unsaturated and exert a pull upon the water in the lower regions of the plant. The rate of rise varies with the season. In summer, when the leaves are fully developed, the transpiration stream may rise at the rate of four or five feet per hour. In autumn, the rate of rise falls off, especially after frosts and freezes which induce leaf fall; and by winter time the rate may not exceed an inch per hour in woody shrubs and trees. Once more in spring, when buds begin to open and leaf expanse is developed, the rate of rise increases until the level of summer rate is reached. There is a fluctuation of the rate of rise because of daily and hourly changes in humidity, temperature, wind flow, and light intensity. Even during rains, it is probable that the transpiration stream continues to move upward. The previous saturation deficit is reduced during a rain, but it is doubtful whether, in the open air, precipitation of moisture can completely stop loss of water vapor from plants. However, if plants are completely surrounded by water until the saturation deficit is fully met, the transpiration stream can be completely arrested.

Transfer in small plants. — In the smaller land plants, whose bodies are composed of living cells throughout, as in many liverworts and mosses, the water has to travel but a short distance, and the movement

can be osmotic only. Evaporation at an exposed surface concentrates the solutions in those cells, thereby reducing the internal pressure of the water, which moves from an adjacent cell to reëstablish equilibrium, and so the disturbance soon reaches the surface cells in contact with free water, which enters the plant.

Origin of a conducting system. — We might infer that these osmotic movements are too slow to afford a proper supply to larger plants, because, as an actual fact, they are in operation for only relatively short distances; the larger the plant and the more necessary a large supply of water, the more perfect and extensive becomes the special system of tissues for conducting water by avoiding osmotic transfer. This is especially striking when one follows the development of such a plant as a sunflower from the embryo, a stage when there is no water-conducting tissue, to maturity, observing how the extent and amount of this tissue increases as the foliage develops and so increases the evaporating surface. The history of the evolution of land plants may be somewhat similar. As the early aquatics became more and more exposed to evaporation, there probably came about the development of structures which limit the water loss, and simultaneously the development of the water-conducting strands, which greatly facilitate water movement.

Elongation of cells. — Presumably one of the simplest expedients to accelerate movement is to reduce the number of membranes which the water must pass osmotically. This could be accomplished to a certain extent by elongating the cells in the main direction of travel; and it may be that elongation of the cells was one of the early steps in the evolution of a conducting system. To-day there are plants in which such strands exist, as in the stalk of the sporophyte of liverworts and mosses, and these are often accounted rudimentary conducting tissues.[1]

Lignified tracheids. — The complete elimination of the cytoplasmic membranes may well have been a second step in evolution. This would make movement more easy by removing just so much resistance from the path. If in addition the walls were altered so as to be more freely permeable to water, movement would thus be further facilitated. That change, known as lignification, is indeed common. Then by thickening the wall only in parts, leaving the rest thin, passage of water through it by way of the thinner areas would be still easier. Strands of elongated cells of this sort constitute the endings of the conducting system in the leaves of almost all plants, and they form almost the

[1] This is based too much on analogy and inference; the experimental evidence is weak.

whole of the characteristic wood in gymnosperms and the conducting strands in pteridophytes.

Tracheae. — One further step attains the condition in the most perfectly developed conducting tissues, namely, the resorption of the greater number of the transverse partition walls between the elements, forming cell fusions of great length, known as ducts, or vessels, or *tracheae*, the latter from their occasional resemblance to the human trachea and the air tubes of insects. Resorption does not usually occur near the endings of the strands in the leaves; and in gymnosperms it fails except in the primary strands. But the other changes do occur, and the elements being cells and not cell fusions are distinguished as *tracheids*. Following the history of any row of cells which is to become a duct, there is first the elongation of the cells; then the unequal thickening of the wall and its lignification, together with the resorption of most of the end walls; and finally the disappearance of the protoplasm. Some such steps as these may also have marked the evolution of the conducting system through earlier ages.

Xylem. — The conducting system in the larger plants now consists of a series of strands known as *xylem strands* or as the xylem regions of the vascular bundles. Physiologically it is more satisfactory to treat the xylem as independent of the phloem, for although they are usually closely associated in their course, they may be independent, and the functions of the two are quite unlike. The xylem strands form a connected series, extending from the root-hair region to the mesophyll of the leaves, among which they branch so extensively that there is

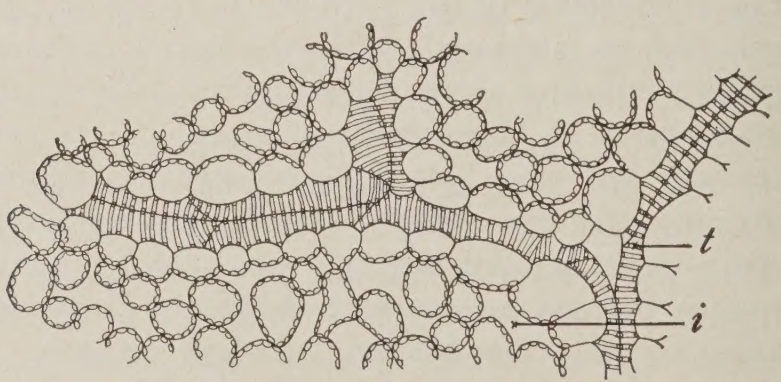


FIG. 23. — Ending of a xylem strand among the cells of the mesophyll in a leaf of lilac (*Syringa vulgaris*): *t*, tracheid; *i*, intercellular space. The cells lining the tracheal cells are the border parenchyma cells.

scarcely a cell which is separated from a strand by more than a half dozen of its neighbors. Here the first branches end blindly (fig. 23)

FIG. 24. — Skeletonized edge of a leaf of a *Ficus*, showing the mode of branching of the smaller veins; the smallest are completely gone. — From a photograph by LAND.

or join their fellows. A section of the root in the root-hair region shows likewise that only a few cells intervene between the free surface and the young xylem strands, which, nearer the root tip, are being differentiated from the plerome. Likewise, a section of the leaf (fig. 11, p. 54) shows the relations of this water-conducting tissue to the surface, and an examination of the venation of various leaves (of which only the larger veins are visible to the unaided eye) shows how extensive is the branching (fig. 24). Between these extremes the bundles run, with lateral connections here and there, especially at the nodes, and more or less variation in size and branching.

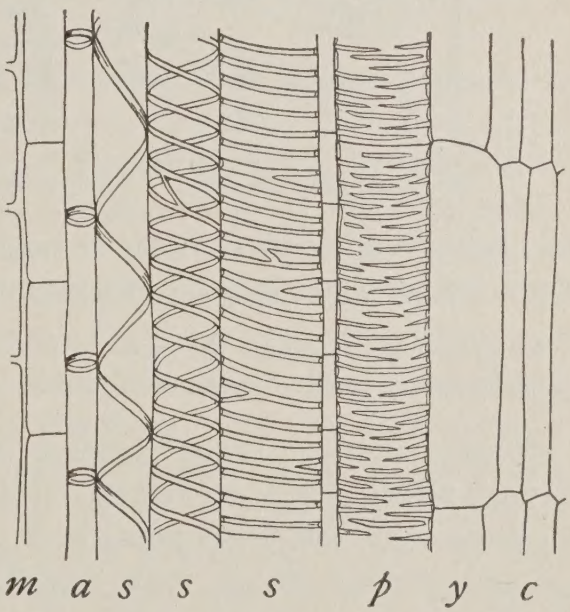


FIG. 25. — Longitudinal section (diagrammatic) of a young xylem strand: *c*, cambium; *y*, young trachea, undifferentiated except as to size; *p*, pitted trachea; *s*, *s*, *s*, spiral tracheae; *a*, annular trachea; *m*, pith. — After HABERLANDT.

Tracheal markings. — The walls of the tracheae are

always peculiarly thickened, the thick regions being in the form of rings, or spirals, or a network (figs. 25, 26). The thin parts may be more extensive than the thick, as in annular and spiral tracheae (figs. 25, *a*, *s*; 26, *s*); or they may be mere spots in the midst of the thick wall, as in pitted tracheae (figs. 25, *p*; 26, *p*, *r*). The thick and

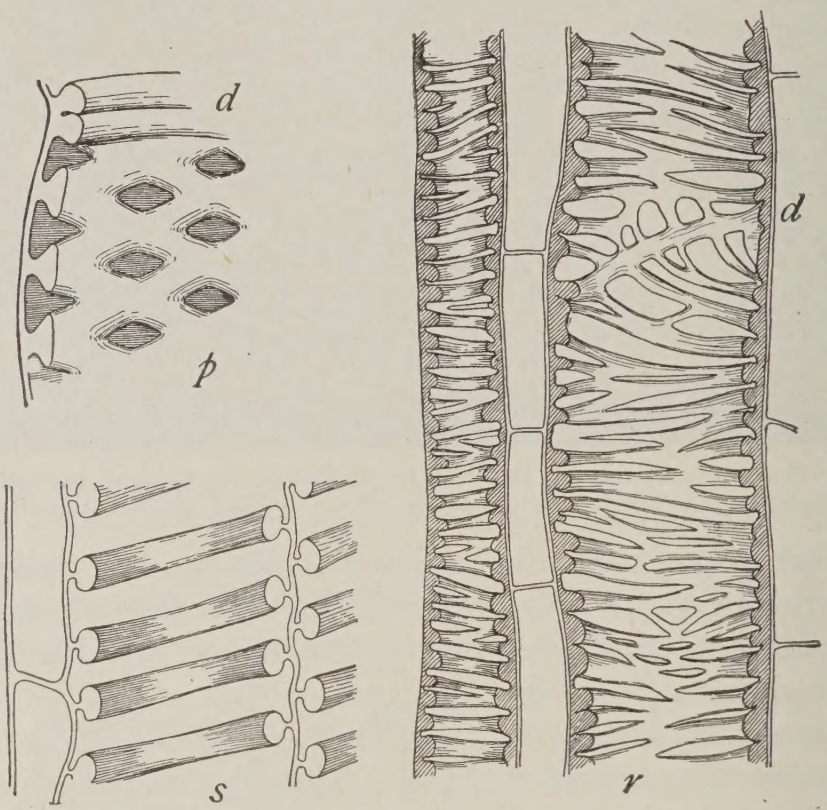


FIG. 26. — Enlarged details of spiral (*s*), pitted (*p*), and reticulate (*r*) tracheae; at *d*, traces of original partition walls. — Adapted from HABERLANDT and TSCHIRCH.

thin parts in adjacent tracheae or tracheids correspond; and thus the movement of water laterally, when conditions require it, is facilitated.

In scalariform tracheids the parts of the wall not thickened are resorbed, and the neighboring cavities communicate freely.

If water in which some cinnabar has been rubbed up be passed through filter paper, to remove all but the very finest particles, and then the filtrate is driven under pressure through a piece of fresh pine wood, the pits become choked with cinnabar, showing that water filters through them more easily and so in greater quantity than elsewhere.

Secondary thickening. — The primary xylem, *i.e.* that differentiated from the young tissue near the growing points (fig. 27), is adequate to supply only the first leaves. As with age the foliage increases, each

primary xylem strand may undergo secondary thickening; *i.e.* it has added to it similar tissues, originating from a layer of dividing cells which adjoins its outer face (fig. 28). In addition, this meristem (cambium), arising between the primary strands, may originate new strands of xylem tissue between the primary ones. These secondary strands may then increase in thickness in the same manner as the primary ones. When numerous primary and secondary strands are produced, they may form a column of xylem, with pith in the center, interrupted by thin radiating plates of parenchyma, the pith rays. Such is the condition in the sunflower, castor bean (fig. 29), and many other dicotyledons.

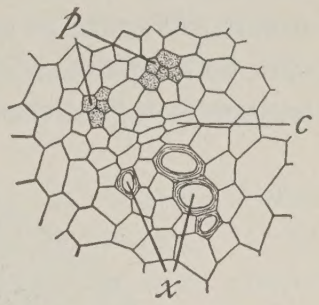


FIG. 27. — Young vascular bundle: *p*, primary phloem; *x*, primary xylem; *c*, first divisions of cambium cells. — After BONNIER. Diagrammatic.

In case the xylem strands do not undergo individual secondary thickening (as is the case in most monocotyledons), there may be a cylinder of meristem which repeatedly produces new bundles, as in asparagus. But in all plants which produce numerous leaves the increasing evaporation is accompanied by an increase of the conducting tissues.

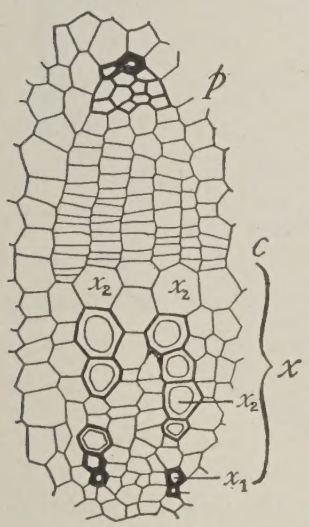


FIG. 28. — Older vascular bundle, with secondary thickening in progress. *p*, phloem; *c*, cambium, forming by division both secondary phloem and xylem; *x*, xylem, composed of x_1 and x_2, the primary and secondary xylem. — After BONNIER.

Annual thickening. — In trees and shrubs the xylem undergoes secondary thickening in the first season of growth, and this is resumed in the second season, and so on, from the persistent cambium. Thus arises a great cylinder of xylem, which constitutes the wood of the trunk and branches. In many trees the xylem formed in the course of the growing season gradually changes its character. The first-formed tissues contain many large ducts and less mechanical tissue, while the later-formed xylem has small ducts and much mechanical tissue. In these cases the open tissues produced in the spring abut on the denser ones last produced in the summer or autumn, and the sharp contrast marks visibly the periodicity in growth. As these differences in the tissue depend upon growth, and as this is most affected by the annual

seasonal changes, the growth rings are usually annual rings, and make possible an estimate of the age of the tree. But annual rings may show subordinate rings, due to some pronounced climatic change which affected the rate of growth more than once in the year. These rings may be so pronounced as to make the age estimate uncertain, but in temperate regions the annual rings are usually well defined. In some

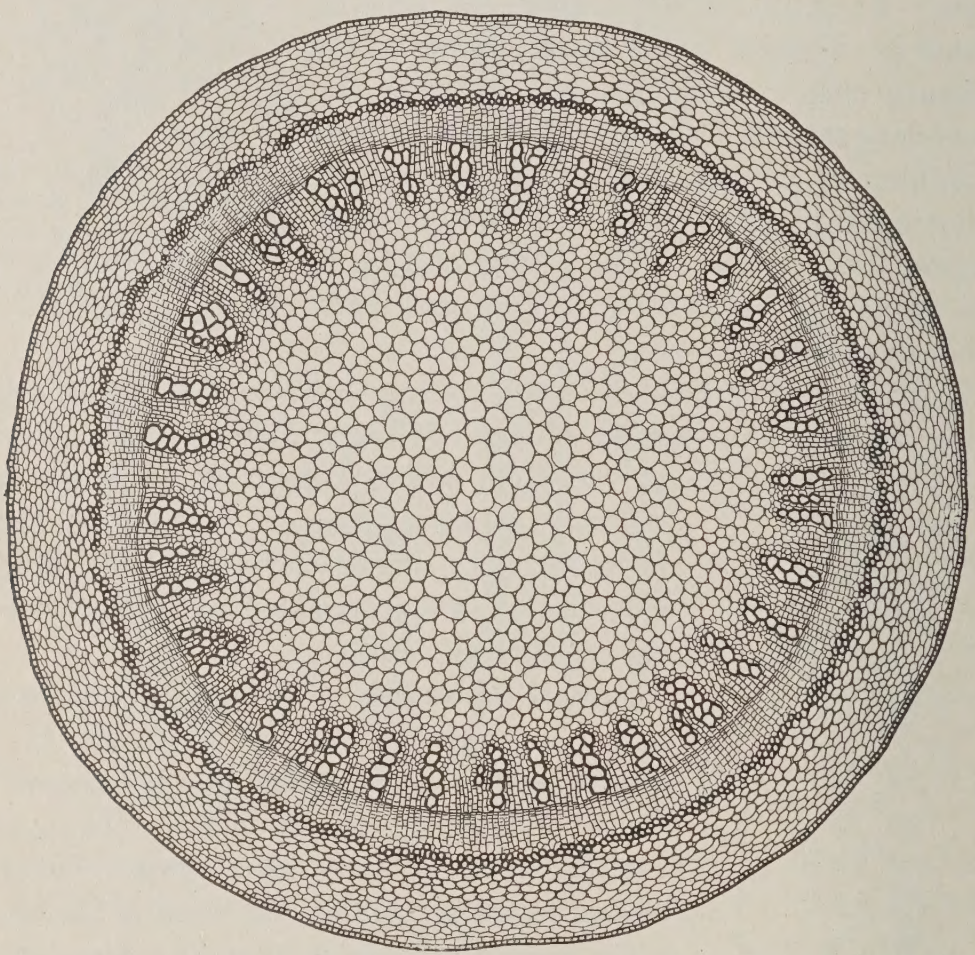


FIG. 29. — Cross section of stem of *Ricinus communis*, showing ring of secondary xylem; for description, see fig. 541.

trees the differences between spring and autumn wood are slight, and the annual rings are discerned with more difficulty. The definite annual rings are responsible in large part for the "grain" of wood. (See also Vol. III, *Ecology*, on annual rings.)

Heartwood and sapwood. — With age the xylem loses its capacity to conduct water, and sooner or later may so change in color and composition as to distinguish the older heartwood from the newer sapwood. These changes, however, do not coincide with the annual rings,

nor do they exactly correspond with the differences in conductivity, since in some plants the whole of the sapwood, but in others only the youngest portion of it, is traversed by the transpiration stream.

Xylem is water path. — The evidence that the xylem is the path of the transpiration stream rests in part upon direct observation, but mainly upon inference from the effects of cutting the xylem strands or blocking the tracheae.

Relative development. — In the first place, one finds a general relation between the amount of transpiration and the development of the xylem. In most submersed water plants the xylem is very poorly differentiated, its place being occupied by some elongated cells, slightly different from their neighbors, which are morphologically equivalent to xylem, but physiologically they are negligible. On the other hand, in climbing plants, whose spread of foliage is large and their stems slender, the xylem reaches its best development, occupying a large proportion of the cross section of the stem, and having ducts of relatively large diameter. Not much reliance could be placed upon such a loose and general relation, were it not for more direct evidence.

Girdling. — Girdling experiments show more clearly the path of the water. It is a matter of common knowledge that by cutting through the sapwood of a tree the foliage promptly wilts and dies; and in earlier days it was commoner than now to see the trees in some piece of woodland "girdled," preparatory to clearing the ground for cultivation. But removing only the bark does not produce wilting, except after weeks or months, for thus only the phloem strands are interrupted. More exact experiments may be performed. By selecting a herbaceous plant whose vascular bundles are distinct, one may cut the pith, the vascular bundles, and the cortex in different specimens and compare the effect. It will be found that only in the specimens whose bundles have been cut do the leaves wilt, and the fact that in woody plants the bark may be removed without causing wilting eliminates the phloem strands. Such experiments permit the inference only that the xylem strands are the chief paths of the transpiration stream, not that they are the sole path; for wilting implies merely an inadequate water supply.

Water moves in the lumina. — But the path can be localized more exactly. A shoot of a climber, such as *Clematis*, may be cut off under water, and the end sliced very obliquely, so as to open wide the ends of

the ducts. If this shoot be fastened to a microscope slide, and the end covered with water, into which has been introduced some finely divided carbon, as from Chinese ink, one may watch the water swirling into the open ends of the ducts, its course being made evident by the opaque particles it carries. Under such circumstances it is evident that the water enters and probably traverses the lumen of the trachea. But this was for a long time a disputed point. When the extraordinary freedom of movement of water in lignified tissues was discovered, it was held that the water traveled in the substance of the walls and not in the *lumina* (the chambers they inclose). This opinion, however, rested upon inaccurate experimentation.

Closing the lumina. — Attempts were made by compressing the stem in a vise to collapse the tracheae, and so to close their lumina. In the earlier experiments of this sort, wilting did not occur, and the inference was plain, therefore, that the water traveled in the wall itself. Repeated studies showed that the difficulty of compressing the tracheae had been underestimated, and that when they were actually closed mechanically, the leaves did wilt. A better method of closing them is by plugging them with paraffin or gelatin which melts at a low temperature. By cutting a shoot under the melted material, it is carried up instantly to some distance in the tracheae. When cooled, it solidifies and a fresh surface of wall can be exposed by removing a thin slice, while the lumina remain plugged. The leaves of such a shoot promptly wilt when exposed to dry air.

Path of least resistance. — On the whole, therefore, it is fairly certain that the transpiration stream traverses the xylem strands, and that it is the lumina of the tracheae that form the chief conduits for the water. That some travel in the walls is quite probable, especially when the tracheae are partly blocked, as they often are, by gas, the path of least resistance being followed here as always. Nor is it impossible that some water moves in the cortex; but this is never enough to cover any considerable loss by evaporation.

Ascent of water. — The problem of the ascent of sap in tall plants has always attracted the interest of plant physiologists, because it seems to contradict some of our notions of the physics of water movement. It presents a very complex and difficult problem, and many unsuccessful attempts have been made to explain sap rise. Some of the early explanations that have been abandoned involved the action of capillarity, root pressure, atmospheric pressure, and the pumping action of living cells. Neither singly, nor all taken together, are these forces adequate to account for the observed facts.

During the last quarter of a century our knowledge of the physical principles involved in the ascent of sap has been so increased as to make possible, now, a fairly satisfactory explanation of the rise of sap, even in the tallest trees. The experimental evidence brought forward by Dixon,[1] Renner,[2] Bode,[3] and others in support of the cohesion theory has convinced many students of plant physiology that this explanation is essentially correct in its main features. This cohesion theory will be presented in detail after considering briefly some of the forces that were urged by earlier students of the problem of sap rise.

Capillarity. — Some " causes " frequently assigned and popular at one time may be definitely discarded. The first of these is capillarity, as commonly understood. The xylem ducts are narrow tubes. Water rises in capillary glass tubes above the level outside, and the smaller the bore the higher it rises. Oil rises in a twisted lamp wick by capillarity. What more simple than to " explain " the rise of water in the ducts of the xylem strands by ascribing it to capillarity, since here are " strands " and " tubes "? But surface tension (which is a better name for capillarity) implies a free surface, and within the duct there can be no free surface which is lifting, as in an open glass tube. If one appeals to the surface bounding the bubbles of gas so common in tracheae (see p. 96), it must be remembered that for every meniscus concave upwards there is one concave downwards to balance it. Nor can one neglect the numerous transverse walls in the xylem of angiosperms,[4] and the fact that all the effective xylem of gymnosperms is composed of tracheids. How surface tension forces may operate at the evaporating surfaces in the leaves is not completely known; but these are not the ones referred to when capillarity is invoked as the cause of the ascent of water, or at least an aid to it.

Root pressure. — Root pressure (see p. 80) is frequently alleged to be active in forcing water up; and it is even held to be adequate in the case of the herbaceous plants and low shrubs, though confessed to be insufficient in the taller trees. The radical difficulty with turgor in the

[1] Dixon, H. H. Transpiration and the ascent of sap. Macmillan Co. 1914.

[2] Renner, O. Theoretisches und Experimentelles zur Kohäsionstheorie der Wasserbewegung. *Jahrb. wiss. Bot.* **56** : 617–667. 1915. Versuche zur Mechanik der Wasserversorgung. *Ber. d. bot. Ges.* **36** : 172–179. 1918.

[3] Bode, Hans Robert. Beiträge zur Dynamik der Wasserbewegung in der Gefässpflanzen. *Jahrb. wiss. Bot.* **62** : 92–157. 1923.

[4] The longest continuous ducts found exceed 5 m., but those 1 m. long are rare, and the average is probably less than 10 cm.

root cortex as a cause of the ascent of water, or at least an aid to it, is that it does not exist when it is most needed. In the very nature of the case the root cortex can be fully turgid only when it has an abundance of water; and it is not likely to have that when evaporation is active. To develop root pressure it is necessary to check evaporation, as by decapitation, and only *after a time* does water begin to ooze from the xylem in consequence of turgor. Often water at first enters the stump of a decapitated plant, showing clearly that there was no surplus of water under previous conditions. Nor can root pressure be invoked even as an aid. For unless maximum turgor can be attained no extrusion of water from cortical cells is possible.

If a boy could push a wagon while the horse walked, he would be unable to push as soon as the horse's speed exceeded his own. If he clung to the wagon, he would be merely a drag, though if he ran he would be less of a drag than if he made no exertion. The transpiration horse often goes too fast with the water wagon for the root pressure boy to push. Then his grip is broken at once and he is no drag on the load, for root pressure cannot even hold on like the boy and " help " by not being wholly a drag.

Atmospheric pressure. — Atmospheric pressure has been invoked as an explanation. It is found that the gases which develop in the tracheae are often under a pressure less than one atmosphere. Indeed they develop there readily because this is the case. The tracheae, it must be remembered, are dead cells; their lumina therefore are as free to be occupied by gases as are intercellular spaces. Whenever the concentration of gases dissolved in a free liquid exceeds the amount normal at one atmosphere pressure, the gas particles escape from solution and form bubbles.

This happens when any bottle of liquid " charged " with CO_2 is opened. The gas is dissolved in the liquid under a pressure greater than one atmosphere; on uncorking it the pressure is reduced immediately to that of the outer air, the gas flashes at once into bubbles, and portions of the liquid are often forced out of the bottle by the violence of effervescence.

Bubbles would inevitably form in the water of the tracheae, whenever that water has the pressure on it reduced below one atmosphere. If this pressure were equal to half an atmosphere, it is argued that such tension could " lift " water about 5 m. So it could, if the lower end of the water columns were open to the pressure of the atmosphere and there were no resistance. If one took away half an atmosphere of pressure from the upper end of a water column and left a whole atmos-

phere of pressure to act on the lower end, of course the water would rise to the point of equilibrium. But these conditions do not exist in the plant. Evaporation may reduce the pressure on the water in the tracheae, but the lower end of the water column is not open. The living cells of the root cortex are interposed, and water cannot be driven through them by a difference of half an atmosphere or even a whole atmosphere of pressure; nor has the pressure in the tracheae ever been found to fall to zero. If it *were* zero, and there were *no resistance* to the movement, water could be pressed up to a height of only 10 m., a small fraction of the 100 m. which the tallest trees attain. Atmospheric pressure therefore is utterly inadequate at best. The most that can be allowed is this: by how much the difference in atmospheric pressure in the tracheae and in the air tends to make it easier for water to pass through the root hair and the root cortex, by so much atmospheric pressure may be said to help in the entry of water. But the very fact that these differences exist shows that they are not compensated by the movement of the water. In fact the difference between inner and outer pressure seems to be rather a result than a cause of water movement.

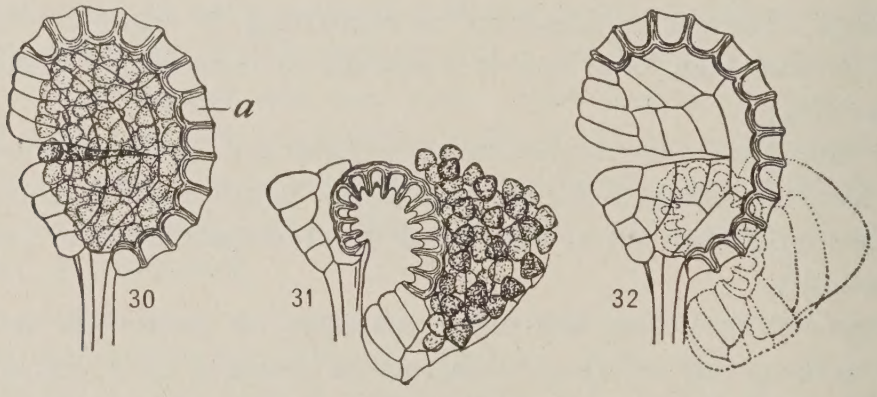
Rôle of living cells. — The ultimate cause of the ascent of sap is transpiration. The energy employed in vaporizing the water is adequate to lift it miles high; but how is it applied so as to keep a continuous stream rising?

One link in the chain is the osmotic relations of the living cells of the leaf; for if the leaves be killed, evaporation continues from their cells, but the supply from the xylem strands is interrupted and the leaf dries up promptly.

It was also proposed, first many years ago, to ascribe the ascent of water to the action of living cells along the course of the xylem strands, and this theory is being advocated again to-day. One notion of their action was that it is like that of relay pumps, which take water in at one level and force it up to a higher level. It is difficult to conceive the physics of such an operation, and there is no anatomical evidence of such a mechanism, unless the cells of the pith rays are the active cells. The experimental evidence as to the coöperation of living cells in the process is contradictory, to say the least, and by its very nature the theory must be rather vague. That the living cortex and wood parenchyma are necessary to keep the xylem in proper condition for conduction is assumed.

Cohesion theory. — The most plausible theory of sap rise is based on the fact that water columns, in the absence of shearing forces, exhibit a remarkable degree of cohesion. Dixon re-examined the problem of water cohesion and found that water columns in small glass tubes would withstand contraction tensions of 150 to 200 atmospheres before actually breaking. He also offered some evidence to show that the cohesion between water and wood is greater than that between water and glass. Other experiments carried out with fern annuli in the presence of known vapor pressures indicate even larger values than these for the cohesion of water in cells and small vessels.[1]

The rupture of sporangia of ferns and the anthers of flowering plants, and the collapse of cells on drying, have now been shown to depend upon the cohesion of water. The mechanism for spore scattering in the sporangium of a fern, for example, is illuminating. It consists of thick-walled cells around the edge, the annulus (*a*, fig. 30), which contain water. As the water evaporates it pulls the cell walls together, and in doing so straightens the ring and tears open the weak side. The thick elastic C-shaped walls of the cells resist this compression, until finally the cohesion of water in the wall with the free water in the lumen is overcome, and the sudden elastic recoil of the annulus hurls the spores as from a sling.



FIGS. 30–32. — Rupture of sporangium of a fern (*Polystichum acrostichoides*): 30, the sporangium cracked; *a*, the annulus; 31, position of complete reversion, many of the spores adherent to the upper part of the sporangium; 32, position after recoil, the sporangium emptied; dotted lines in this figure show the position as in 31. — After ATKINSON.

By determining the vapor pressure at which the elastic recoil of the annuli occurs, it has been shown that the cohesion of the water in the annulus cells runs as high as 300 to 350 atmospheres. These values must be considered minimal values, because it is probable that breaking

[1] Ursprung, A. Über die Kohäsion des Wassers im Farnannulus. *Ber. deutsch. bot. Ges.* 33 : 153–162. 1915.

occurs before the maximum possible cohesion is developed. There is no reason for supposing that the cohesion of water in the tracheae is any less than that in the fern annulus cells, and Dixon's measurements on plant saps exceed 200 atmospheres.

In order that sap rise may be explained, there must be an adequate force somewhere to push or pull the water to such great heights. It is generally conceded that the force is a pull from above. There must also be a means of transmitting the pull from cell to cell to the upper end of the columns of water in the tracheae, and a renewal of the water supply at the lower end of the tracheae by the root system. These problems will now be considered.

The lifting power. — The forces which lift water from the roots to the leaves of plants are developed in consequence of the evaporation of water from the intercellular surfaces of the leaves. They reside, first of all, in the walls of cells from which the evaporation actually takes place. We cannot properly speak of the evaporating power of the air, for water evaporates much more rapidly in a vacuum than in ordinary air. Evaporation is the result of the kinetic activity of the water itself, the degree of kinetic activity depending upon the given temperature. Water molecules are constantly jumping out of the water surface and migrating into the air as water vapor, because the air has a lower vapor pressure than the water and thus forms a partial water vacuum into which the water evaporates.

As evaporation occurs from the cell walls of the leaf, the substances of which the walls are composed become drier. They become somewhat less than saturated with water, and we say they develop a saturation deficit, or water deficit. This development of water deficit brings into play the powerful surface attractions of the colloidal materials of the cell walls for water. Being partially dried, they can imbibe fresh supplies of water; but the only way in which these cell walls can secure another supply of water is to obtain it from the living protoplasm which lies in contact with the walls. The result is that the wall colloids take water from the protoplasmic colloids within them, and so the protoplasm also develops a saturation deficit. The protoplasm in turn secures additional supplies of water from the vacuole which it surrounds. The net result of all these changes is that the whole external portions of the leaf system are placed in a condition of water deficit, or partial dryness, that exerts a pull upon any available source of water.

There would be no exertion of this pull on the water in the tracheae of the vascular system if it were not for the surface attractions of the colloidal substances of the leaf for water. These colloidal surfaces serve as the fulcrum upon which the pull depends. If this were not true, during evaporation the water would simply recede deeper and deeper into the leaf, without exerting any upward pull. As it is, when the colloidal materials lose their water, the surface molecular and ionic forces pull upon the water farther back in the leaf, and, in conjunction with the kinetic tendency of water to move from places of high water content toward places of lower water content, from moist toward dry, the water is brought from the interior of the leaf toward the surface where evaporation is occurring.

This pull is very large if much drying occurs. It is estimated that the maximum kinetic force of water molecules at ordinary temperatures is about 1350 atmospheres.[1] This is based on the fact that a liter of water would contain 55.5 gram molecules of liquid unassociated water. As the leaf dries out, its vapor pressure is lowered, and a lowering of the vapor pressure of the intercellular walls and protoplasm of the outer cells by only 7 per cent [2] may cause a pull of 100 atmospheres upon the water farther back in the leaf. This is much more than is needed for sap rise, even in the tallest trees.

We may think of the lifting force, then, as the force developed in drying gel colloids of the leaf by evaporation of water, a force that can develop an enormous pull. Drying gelatin, for instance, will scale off glass from the surface of Petri dish or watch glass, or break the bottoms out of beakers, due to the enormous forces of drying.

Transmission of the pull. — If we consider the cell walls bounding intercellular spaces, and the protoplasm in contact with them as the seat of the lifting power of evaporation, then there must be some way of transmitting this pull back into the deeper regions of the leaf, and to the tracheids and tracheae of the vascular system.

This transmission of pull is brought about mainly by osmotic action. When the protoplasm takes up water from the vacuole which it surrounds, it removes mainly pure water, and so tends to concentrate the vacuolar solutes. There is less water per unit volume in such concentrated solutions than in more dilute ones, and more interference with the

[1] Shull, Charles A. *Loc. cit.* (See p. 81.)

[2] Renner, O. Theoretisches und Experimentelles zur Kohäsionstheorie der Wasserbewegung. *Jahrb. wiss. Bot.* **56**: 617–667. 1915.

outward diffusion of water. This would lead at once to the passage of water from adjoining cells into the one whose vacuole had lost water, provided they had a larger proportion of free water in their cell sap. Wherever we have vacuole-containing cells in contact with one another, water is tending to distribute itself in accordance with its own concentration and the colloidal forces of the more solid parts of the cells. If water flows from adjacent cells into those that lose water, then they in turn set up osmotic migration of water from cells still further back. Finally we find the water moving from the border parenchyma cells into the leaf mesophyll, and these border parenchyma cells drawing their own supplies of water from the tracheids and tracheae of the water-carrying system. The series of cells between the xylem and the evaporating surfaces constitute a chain of osmotically active cells which transmit the evaporational pull to the tracheal system.

Osmotic concentration of leaf cells. — We must now examine the facts regarding the osmotic pressure of leaf cells, with the object of determining whether there is force enough in the osmotic action of leaf cells to accomplish the lifting of water from roots to leaves. Careful determinations of the osmotic pressure of leaf cells by both plasmolytic and freezing point depression methods [1] show that the osmotic concentration of leaf cell sap is often high, and that it varies with climate and habitat [2] in such a way that the osmotic forces are nearly always larger when the work to be done is greater. In a lilac bush for instance, we may find the osmotic concentration equivalent to 25 atmospheres. But in a dry region the values run much higher than that. Thus Fitting [3] found that in the Sahara Desert about one third of all the species examined had osmotic concentrations in excess of 100 atmospheres. In salt marsh regions, where the roots are surrounded with solutions more concentrated than usual, the leaves of plants growing in these marshes show sap concentrations of 40 to 50 atmospheres. The same is true of plants growing in alkali spots in arid regions. The

[1] Harris, J. A., and Gortner, R. A. Notes on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing point, with a table for the values of P for $\Delta = 0.001°$ to $\Delta = 2.999°$. *Amer. Jour. Bot.* **1** : 75–77. 1914. See also *Amer. Jour. Bot.* **2** : 418–419. 1915; and **12** : 499–501. 1925.

[2] Harris, J. A., Lawrence, J. V., and Gortner, R. A. The cryoscopic constants of expressed vegetable saps as related to local environmental conditions in the Arizona deserts. *Physiol. Res.* **2** : 1–49. 1916.

[3] Fitting, H. Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. *Zeitschr. Bot.* **3** : 209–275. 1911.

highest osmotic concentration ever reported for plant saps runs about 205 atmospheres, and was reported for a species of mangrove growing in the East Indies.[1] Woody plants usually have saps of higher osmotic concentration than herbaceous plants growing in the same habitats. Leaves high up on a tree usually are found to have more concentrated solutes than those farther down the tree.[2] Where parasites like mistletoe grow on a tree, we usually find that the parasite has an osmotic concentration of its leaf cell sap that enables it to secure water from its host plant.[3]

Students interested in these problems should consult the numerous papers of Harris and his coworkers on this subject. *See Jour. Agr. Res.* **27** : 922–924. 1924, for citations.

Careful investigations have thus shown a close correlation between osmotic concentration and the lifting force required for the work done.

Magnitude of force required. — Will the osmotic pressures observed suffice to lift the water, especially in tall plants? Before we can answer that question, we must ascertain how much force is needed to lift water in a 300 to 400 foot tree. Since the force of the atmosphere will lift a water column only 32 feet, it is clear that we would require a lifting force of 10 to 12 atmospheres just to lift the column of water to such great heights. But in addition to mere lifting, there is friction to be overcome, for the water passes through very small tubes during its rise. Dixon's tests of the force required to overcome friction showed that it took just about as much force to overcome the friction as to do the lifting, so that we should have to employ forces of 20 to 25 atmospheres to lift the water against the force of gravity and the frictional resistance of the xylem, in trees of such great height. In addition, we must remember that the root cells have some osmotic pressure. According to Hannig,[4] these average about 8 atmospheres, so that we

[1] Harvey, E. M. The fourth Pacific Science Congress. *Plant Physiol.* **5** : 1930.

Harris, J. A., and others. Maximum values of osmotic concentration in plant tissue fluids. *Proc. Soc. Exp. Biol. and Med.* **18** : 106–109. 1921.

[2] Harris, J. A., Gortner, R. A., and Lawrence, J. V. The relationship between the osmotic concentration of leaf sap and height of leaf insertion in trees. *Bull. Torrey Bot. Club.* **44**: 267–286. 1917.

[3] Harris, J. A. On the osmotic concentration of the tissue fluids of desert Loranthaceae. *Mem. Torrey Bot. Club.* **17** : 307–315. 1918.

Harris, J. A., and Lawrence, J. V. On the osmotic pressure of the tissue fluids of Jamaican Loranthaceae parasitic on various hosts. *Amer. Jour. Bot.* **3** : 438–455. 1916.

[4] Hannig, E. Untersuchungen über die Verteilung des osmotischen Drucks in der Pflanze in Hinsicht auf die Wasserleitung. *Ber. deutsch. bot. Ges.* **30** : 194–204. 1912.

must have forces of 28 to 33 atmospheres to do the lifting in our tallest plants. From the osmotic concentrations found in leaves there is no reason to doubt that we have such forces available for the work in these cases. In a plant not more than 32 feet tall, an osmotic concentration of 10 or more atmospheres is sufficient, for the lifting would require 1, the resistance 1, and the root cells average about 8 atmospheres. Since we nearly always find osmotic concentrations in leaves considerably in excess of 10 atmospheres, there is sound reason for believing that osmotic pressure not only serves to transmit the pull developed in the gel colloids of cell surfaces back to the upper ends of the tracheae of the xylem system, but it is adequate quantitatively to pull those columns of water up the tree. The cohesion of the columns is far greater than the pull, so that they can be lifted without breaking.

Negative pressures in stems. — If the leaf region suffers evaporational loss of water at a rate faster than the root can obtain a supply from the soil, negative pressures are developed in the water transporting system. Such negative pressures have been demonstrated, and their effects observed, even if it is difficult to produce and maintain them artificially in cut plant stems. One evidence of negative pressures produced in plant stems is the expanded condition of air bubbles in the xylem tubes. A wilty plant cut under eosin dye will show a rapid rise of dye in the tracheae, whereas if cut first in air and then put into the dye, the rise of eosin is very slow, because air has been drawn into the cut ends of the tracheae on contraction of the gases when the plant was cut. This shows the existence of negative pressures in the plant stem. There is no doubt that the evaporational tension on the tracheal water columns causes negative pressures in stems.

MacDougal [1] has shown by the use of the dendrograph, an instrument for recording changes in the diameter of trees, that the trunks of trees decrease in diameter during the afternoon when evaporation is high, and increase in diameter at night, when root absorption exceeds evaporation. The shrinkage during high evaporation may be partly caused by colloidal dehydration throughout the aërial parts of the plant; but it is hardly to be doubted that, in part, the shrinkage is caused by the tension on the tracheae, which tend to become narrower under the stress of transpirational tension. Bode [2] has observed plants

[1] MacDougal, D. T. Growth in trees. *Carnegie Inst. Pub.* No. 307. Washington. 1921. See also *Scientific Monthly* **21**: 99–103. 1925.

[2] *Loc. cit.* (See reference 3, p. 95.)

under the microscope, and has watched the gradual narrowing of the xylem tubes as the tensions develop. He has also observed that there are no air bubbles developed in the tracheae during the development of tension, so that we have unbroken columns of water under tension.

Such effects and observations as are mentioned here, indicating negative tensions in stems, are favorable to the cohesion theory of sap rise.

Breaking the water columns. — Of the several forces involved in sap rise, evaporation, osmotic forces, cohesion, the first is by far the largest. It may reach a thousand atmospheres in air of average relative humidity. Osmotic forces, we have seen, do not exceed 200 atmospheres except in rare cases, and are usually between 10 and 100 atmospheres. Cohesion may run as high as 300 to 350 atmospheres, but often it is overcome before these high values come into play. If the water column contains gas in solution, it may break by gas coming out of solution especially as the temperature rises; or other conditions may cause breakage, as agitation by wind currents. When a plant wilts, great stress is placed upon the water columns. As long as these do not break, the plant will recover on being watered. But if wilting becomes so severe that the water columns are broken by the pull from above, the wilting becomes permanent, and the plant dies.[1]

The root system and sap rise. — What part does the root play in the process of sap rise if the pull comes from above? The whole structure of the root system indicates that it is made to take in water readily from the soil solution, and transmit it to the lower end of the tracheae. No very adequate explanation of how the root pours water into the tracheae below has ever been presented. Several ideas have been suggested:

(1) The whole system of living cells in the root region is thought by some to act like a single semipermeable membrane, the inner cortical layer, the endodermis, serving as the basis of this membrane.[2] The unidirectional transfer of water is likened to excretion, the water being allowed to enter the tracheae because the last living cells that bound the tracheae are more permeable to water and solutes on the side next the tracheae. While such excretion has been observed in glandular hairs, where the last cell seemed to be more permeable

[1] Bakke, A. L. The index of foliar transpiring power as an indicator of permanent wilting in plants. *Bot. Gaz.* **60**: 314–319. 1915.

[2] Priestley, J. H. (See citation, p. 81.)

than the rest and allowed excretion of water, no proof exists that the root cells have any such behavior.

(2) It has been pointed out by students of membrane permeability that the electrical conditions of the membrane may give rise to a unidirectional transfer of water across the membrane. This is called electro-osmose.[1] There is no question that in certain membranes, and under appropriate electrical conditions, such transfer of water in one direction across the membrane really occurs. But, again, we have no indications that this factor comes into play in root cells. It has not even been investigated, but is a possibility.

(3) Ursprung[2] recently has claimed that the cells of the endodermis act as though they had a higher osmotic action on one side than on the other. He speaks of a polarized osmotic flow, the cells drawing water in on one side and forcing it out on the other. This seems rather improbable, and should be taken with great caution until the results have been confirmed, or disproved.

(4) Osmotic pressure can be reversed across a membrane. By exerting a positive pressure upon a solution separated from its solvent by a semipermeable membrane, pure solvent can be driven back out of the solution into the solvent, against the osmotic flow. This has actually been demonstrated by Lord Berkeley and Hartley.[3] If the flow can be reversed by a positive pressure on the one side of the membrane, it should also be reversible by a negative tension applied to the other side of the membrane. We have just seen that the tracheae may be the scene of considerable negative tension. If this negative tension exceeds the osmotic pressure of the innermost living cells of the root, water should be pulled into the tracheae under the influence of this negative cohesional pull, against the force of osmotic pressure operating in the opposite direction.

The root system probably transfers water from soil particle to tracheae by means of osmotic action, just as in the leaf the water movement is osmotic. The root system can hardly be looked upon as merely a passive strainer through which evaporational tension pulls water, although this idea has been suggested by some. It seems better to

[1] Bartell, F. E. Membrane potentials and their relation to anomalous osmose. *First Colloid Symopsium Monograph.* 120–135. 1923.

[2] Ursprung, A. Proceedings of the fifth international congress of plant sciences. Ithaca. vol. II. 1081–1094. 1926.

[3] Berkeley, Earl of, and Hartley, E. G. J. On the osmotic pressure of some concentrated aqueous solutions. *Phil. Trans. Roy. Soc.* Lond. A. **206**: 481–507. 1906.

consider it an active system, which sometimes delivers water faster than the evaporation removes it, thus producing root pressure, and bleeding, and at other times delivering the water less rapidly than physical conditions cause evaporation to take place. Then wilting occurs, temporary or permanent, according to the severity of the evaporational excess over root absorption.

The cohesion theory as it has been developed by Dixon, Renner, Bode, and others, seems at present to be the most acceptable theory of sap rise. It is supported by much detailed evidence, and it seems to satisfy all the requirements. Occasionally the pumping action of living cells is still urged, and in a recent book Bose [1] has contended that the cortex pumps the water upward by a sort of hydraulic wave motion. There is as yet no sound evidence for this suggestion, and most plant physiologists feel that it is without foundation.

4. OTHER LOSSES

Gases from the shoot. — Quite apart from the liquids and water vapor which escape from the aërial parts, there are gases which are constantly set free and leave the plant as such. These are carbon dioxide and oxygen, and in some instances ammonia and trimethylamine. The former is one of the usual end products of respiration, and the oxygen is a by-product of food making, but is used by all live parts in respiration. Carbon dioxide is continually produced in all live parts; but in green parts, when adequately lighted, it can be used for making food, and therefore in these parts under such conditions it never accumulates to an amount which permits it to diffuse out. Oxygen is only intermittently produced. When the green parts are making certain foods, its production is a measure of their activity; but that takes place only in the light. Since, therefore, the leaves are the green parts *par excellence*, oxygen escapes chiefly from them, because the amount produced is in excess of that used in their respiration. When it has accumulated in the cell sap to a concentration whose osmotic pressure is greater than its pressure in the air (*i.e.* about 0.2 of an atmosphere, or 152 mm. of mercury), it will fly off as a gas from the surface of the cell into the internal atmosphere of the aërating system. Likewise when carbon dioxide has accumulated to a suitable pressure (less than 0.0003 A., or about 0.22 mm. Hg.), it begins to diffuse into the air. Trimethylamine and ammonia are given off in gaseous form

[1] Bose, J. C. *The Physiology of the Ascent of Sap.* Longmans, Green & Co. 1923.

by cotton plants, from flowers of certain of the Rosoceae, and from the leaves of a few other species.

Diffusion from the root. — Oxygen can be formed only in green parts and hence probably escapes only from aërial parts although it has been suggested that some oxygen may diffuse out through the root during rapid photosynthesis.[1] Carbon dioxide, being formed in all live cells, can also escape through the other permeable region, the root. Its escape there may be directly into the soil water, whenever it has accumulated to a greater pressure in the cell sap. To demonstrate diffusion it is only necessary to grow the roots in contact with a polished marble plate (calcium carbonate), whose surface will be etched along the lines of contact because water, "carbonated" by the CO_2 escaping from the roots, converts the calcium carbonate ($CaCO_3$) into calcium bicarbonate [$Ca(HCO_3)_2$], which is readily soluble. Or by growing seedlings in water with phenolphthalein (an indicator which is rose red in weak alkaline and colorless in acid solution), the water will be decolorized by the roots; but the color will return upon boiling, which drives off the CO_2 which had united with the indicator. Were any mineral or organic acids the cause of the decoloration, the color would not return.

But besides CO_2 other substances may leave the plant by way of the roots. At present these are not accurately known. Water cultures made with soil extracts indicate that organic compounds, often very deleterious to the culture plants, are frequently present. These may have come into the soil by diffusion from roots (see p. 35). Acid salts, such as hydrogen potassium phosphate, are probably not among the exudates, as once they were believed to be. Yet any substance in the root cortex, to which the cells are permeable, may escape; and when the matter is studied further, many compounds, now unsuspected, may be found diffusing into the soil water.

Mechanical losses. — Mechanical losses must also be taken into account. In all plants the drying of leaves, flower parts, rootlets, and even larger parts of the body, is followed sooner or later by their falling off. In annuals, the whole body perishes at the end of the growing season; hence the perennials offer the best examples. In woody perennials, particularly, the partial fall of the leaves in summer, due to heat, drought, or other causes, and the complete autumnal fall, are striking losses of material. Yet this is not so expensive to the plant

[1] Hutchins, L. M. Studies on the oxygen-supplying power of the soil, together with quantitative observations on the oxygen-supplying power requisite for seed germination. *Plant Physiol.* 1: 95–150. 1926. (See especially p. 145.)

as it might seem at first sight, for a large part of the available foods have been transferred from the leaves before their fall, and what is left is chiefly cell-wall stuff, unavailable organic matter, and ash. Nevertheless, much of that represents past expenditure of energy and is a dead loss; though by decay some of the materials again become available for rebuilding.

Fall of leaves. — The once active food-making machines go to the scrap heap in autumn and have no value except as junk. Their deterioration is progressive. In the leaves of woody plants as compared with other parts, there is with age, as a rule, a steady accumulation of dry matter and a rising proportion of ash.

Thus in the leaves of the European beech (*Fagus sylvatica*):

	May	June	July	Aug.	Sept.	Oct.	Nov.
Per cent dry matter . .	23.35	40.21	43.64	50.74	47.42	40.37	45.55
Per cent of ash	4.67	5.20	7.45	9.03	8.90	10.80	11.42

In black locust (*Robinia pseudacacia*):

	May	July	Sept.	Oct.
Per cent dry matter	26.50	35.90	44.30	44.60
Per cent of ash	6.25	7.75	8.22	11.74

In 500 leaves of the plane tree (*Platanus orientalis*):

	June	July	Aug.	Sept.	Oct.
Grams dry matter . .	142.53	184.70	182.80	193.85	196.24
Grams of ash.	8.70	14.62	17.81	20.12	21.33

Contrast with these figures the average ash content of the wood of such trees, which is about 0.7 per cent, with a minimum of 0.2 per cent and an occasional maximum of about 3 per cent.

This high ash content of leaves is not due merely to the retention of mineral matters when the water evaporated, as lime scale accumulates in a tea kettle.[1] Rather the using of certain constituents of the salts, particularly the nitrogen, sulphur, and phosphorus, left behind the bases, calcium, magnesium, etc., ready to enter into new combinations and to reappear in the ash, when the organic matter is burned away, as CaO, MgO, etc. Moreover, certain mineral salts may be stored in the walls, as silica often is; and these reappear as oxides in the ash.

Fall of branches. — In woody perennials the competition between branches is so severe that many more die than survive. Thousands of rudimentary branches (as buds) never develop at all, and other thou-

[1] This is further evidenced by the fact that the veins of leaves are usually richer in ash than the mesophyll.

sands, after growing for a year or two, are outstripped by their more fortunately situated fellows, die, and drop off. The mortality is vastly greater than is realized without close observation, such as was made on a volunteer black cherry, and described in figurative language thus:

> The first year it made a straight shoot nineteen inches high, which produced twenty-seven buds. It also sent out a branch eight inches long which bore twelve buds. The little tree had, therefore, enlisted thirty-nine soldiers for the coming conflict. The second year twenty of these buds did not grow. Nineteen of them made an effort, and these produced three hundred and seventy buds. In two years it made an effort, therefore, at four hundred and nine branches, but at the close of the second year there were only twenty-seven branches upon the tree. At the close of the third year the little tree should have produced about thirty-five hundred buds or branch germs. It was next observed in July of its fourth year, when it stood just eight feet high; instead of having between three and four thousand branches, it bore a total of two hundred and ninety-seven, and most of them were only weak spurs from one to three inches long. It was plain that not more than twenty, at the outside, of even this small number could long persist. The main stem or trunk bore forty-three branches, of which only eleven had much life in them, and even some of this number showed signs of weakness. In other words, in my little cherry tree, standing alone and having things all its own way, only one bud out of every hundred and seventy-five succeeded in making even a fair start towards a permanent branch. And this struggle must have proceeded with greater severity as the top became more complex, had I not put an end to its travail with the axe! — Bailey: *Survival of the Unlike*, p. 88.

Loss of bark. — The constant flaking-off of bark, when the warping due to wetting and drying loosens the outer portions, or the steady weathering of the solid bark, occasions further losses of a relatively inexpensive kind. As in some cases waste products accumulate in the bark, this may be accounted one way by which the plant gets rid of wastes. Bark also contains a very large percentage of ash.

Fruits and seeds. — Fruits and seeds are separated annually from the body. These are loaded with surplus food for the embryo, and so constitute a most expensive loss — one that not infrequently distinctly impairs the vitality of the plant. The intermittent bearing of orchard trees, vines, etc., may herein find a partial explanation.

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CHAPTER III — NUTRITION

1. THE NATURE OF PLANT FOOD

Food in general is organic. — The question, what is food for plants, elicits very different answers according to the point of view. The term *food* is not one which admits of accurate definition, and the difficulty increases the wider the range of organisms to which it refers. A lion obviously lives upon flesh, and the general constituents of his food can be determined. A sheep feeds on herbage, and that can be analyzed. A man consumes meat and vegetables of the most varied sorts. A fungus like *Penicillium*, which will grow on a glass of jelly or an orange or a piece of cheese or a plate of gelatin, obviously feeds upon vegetable or animal substances indifferently. The nutritive constituents of flesh and vegetables are many and diverse; plainly the term which is to include them must be most general. That term by common consent is *food*. It represents the totality of substances which nourish an organism and enable it to pass successively through the phases of its normal development. Now all the substances referred to belong to a category known as *organic*, because they are all produced by the chemical processes in a living organism. Food, therefore, for the lion, the sheep, the man, the mold, is composed of organic substances. It is true that there are also, in the very organic substances themselves and dissolved in the juices which make part of them, mineral salts of various kinds, and that these are indispensable to living beings; but their amount is very small indeed, and alone they are quite incapable of sustaining life. For the present, therefore, they may be left out of account.

Is the food of green plants inorganic? — The beings enumerated represent all sorts of organisms except the green plant. When we ask, "On what does the green plant feed?" the answer, based on analogy, has been, "On the substances that enter it — water, mineral salts, and carbon dioxide; for with these alone it can develop from embryo to maturity." These are inorganic substances; and if the answer be true, the food of green plants is inorganic and that of all other beings organic.

Is "food" food only for certain cells? — The first thing that awakens suspicion as to the wisdom of this answer is that the living matter of green plants is like that of all other living things, and it would be very strange if in them protoplasm could be nourished with inorganic substances, when in all others it requires organic material. Yet the green plant *might* be differently constituted; and it is said by way of explanation that this peculiarity is due to the presence of the green pigment, chlorophyll. On examining this point, it is found that only a part of the plant has chlorophyll. Most roots entirely lack it; only the outer cells of the stem ever contain it; and there are many cells, even in a thin leaf, and a great mass of them in a fleshy leaf, which are not green. Then we are forced to state the matter thus: the green parts of green plants use inorganic "food"; the colorless parts require organic food, for it is conceded on all hands that the colorless cells are unable to utilize any carbon dioxide and water. Whence it would seem that one cell might nourish itself with inorganic "food" and its next neighbor be unable to do so. That would certainly be a confusing situation if it could not be better described.

Is "food" food only at certain times? — It appears, further, that carbon dioxide and water can be "foods" only part of the time; namely, when the green cells are adequately lighted. So except in the day, even the green cell would require organic food! The situation would have to be stated thus: The "food" of the green cells only, and only by day, consists of carbon dioxide and water; the rest of the plant all the time and the whole of the plant at night must have organic food like all other living things.

Antithesis avoidable. — A little consideration shows that the apparent antithesis between green plants and other creatures is of our own making; it is produced solely by the application of the term *food* to the substances which enter the body, irrespective of their rôle. This antithesis can be avoided, and the confusion and contradiction eliminated, merely by avoiding this inept use of the term *food* and by applying it to organic substances only. By this expedient we escape a different use of the same terms in plant and animal physiology, with its resultant confusion of ideas, and we bring the green plants into line with all other beings, so far as nutrition is concerned. Excluding the inorganic substances from the category of foods, we need to recognize that one power possessed by green plants is unique: they alone make their own food, and not their own only, but food for the whole world. What they use

for this food making — carbon dioxide and water — may be distinguished as food materials. What they make is universally known as food for their colorless cells, for non-green plants, and for animals. Why should it not also be recognized as their own food?

Food for plants is organic. — Food for plants, then, is like food for animals, always organic, the product of living beings; and in the last analysis, nearly all food is made by green plants, for they almost alone among living beings have the power of making it out of the simple compounds CO_2 and H_2O. They make it only in the green cells by the aid of light; and they make so much that they feed not only themsevles, but all other creatures. The lion may live exclusively on flesh, but the flesh was built up by the herbivorous animal from the herbage it grazed, and the herbage was nourished by the foods it could itself make in sunlight. Man grows plants and appropriates the leaves, the roots, the stems, the fruits, or the seeds, improved by his selection and loaded with surplus food, for his own nourishment; or he feeds the steer, the sheep, and the hog with grass or grain that he may later use their flesh for his food.

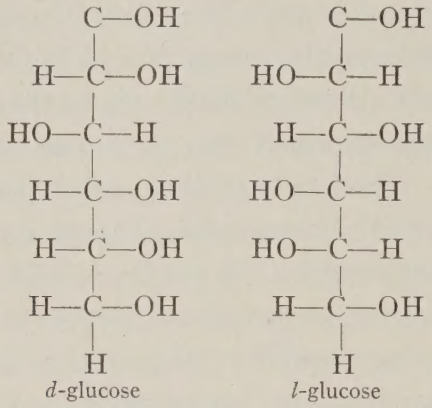
What are the plant foods? — Having established a general meaning for the word *food*, the next question is: To what specific substances is it to be applied? Foods come from many sources and are of many kinds; and because they are so various, only the principal classes can be named, and a few examples briefly described. The four most important sorts are carbohydrates, fats, amides, and proteins.

Carbohydrates. — Some carbohydrates are directly made by green plants; but there are also many that are secondary products. The name is no longer used in chemical classification; it is rather convenient than exact, just as "cryptogam" among plants or "invertebrate" among animals. Here belong the sugars, the starches, and the celluloses, each probably comprehending an indefinite number of different individuals. This is certain among the simpler sugars, whose composition is known; but only hypothetical for starch and cellulose, whose complexity has hitherto baffled all analysis.

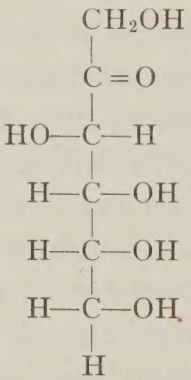
All these substances have a composition like this: $C_nH_{2n}O_n$, or $C_nH_{2(n-1)}O_{(n-1)}$, or $C_nH_{2(n-2)}O_{(n-2)}$, in which the value of n is 5 or 6 or a multiple of these where known, but may run up to several hundred. Thus grape sugar and its allied hexoses all contain $C_6H_{12}O_6$; while cane sugar and its allies consist of $C_{12}H_{22}O_{11}$. Starch and cellulose can be represented only as $n(C_6H_{10}O_5)$, with the value of n quite uncertain, but large. These empirical formulas, however, cannot convey any idea of the complexity of even the simplest carbohydrates, nor of the fact that a mere difference in the position of certain

atoms or groups of atoms, which does not affect the percentage composition at all, gives wholly different chemical and physical characters to the substance.

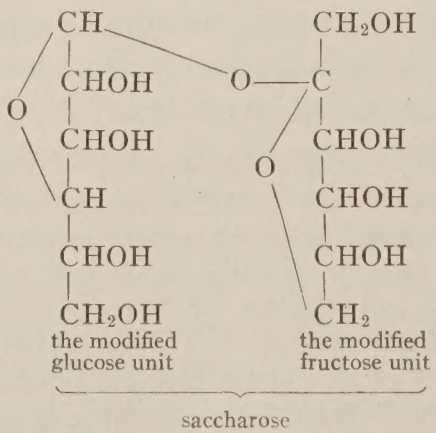
Thus, grape sugar (glucose) exists in two forms, one of which rotates a beam of polarized light to the right and the other to the left; the one, *d*-glucose, is abundant in plants; the other, *l*-glucose, does not occur in nature but has been made artificially. The difference is shown partly in the three following structural formulas, which all sum up $C_6H_{12}O_6$:



Further, fruit sugar (*d*-fructose) is abundant in plants, and its structure is quite different from glucose:



Another sugar especially abundant in plants, cane sugar, $C_{12}H_{22}O_{11}$, probably has this formula:



and when it breaks at the —O— bond, it takes up H·OH and resolves itself into a molecule of glucose and a molecule of fructose. These two hexose sugars, glucose and fructose, and the disaccharide, cane sugar, are the only sugars which occur in abundance in plants; though mannose, galactose, and maltose are formed in the course of digestion.

The simplest carbohydrate building unit which is believed to be formed in plants is formaldehyde, HCOH. This group will be recognized in the makeup of all the more complex ones above (but see pp. 137–139). While it has only a transient existence and does not occur free, except in minute amounts, it has its special significance in that it is probably the first substance formed by the green cells from H_2O and CO_2.

Fats. — Fats are apparently always secondary products, and constitute a common form of surplus food. These storage products furnish various commercial oils; *e.g.* olive oil, cotton seed oil, linseed oil, castor oil, corn oil, etc. They occur usually in fluid form as minute droplets in the protoplast, only occasionally being solid at ordinary temperatures, as in the seed of cacao. They are of very complex structure, being compounds of gylcerin and three molecules of fatty acid.

Their structure may be understood from these formulas:

$$\text{Glycerin is: } \begin{array}{l} CH_2OH \\ | \\ CHOH \\ | \\ CH_2OH \end{array} \qquad \text{A fat is: } \begin{array}{l} CH_2 \cdot R \\ | \\ CH \cdot R \\ | \\ CH_2 \cdot R \end{array}$$

in which R may represent oleic acid ($C_{18}H_{34}O_2$), linoleic acid ($C_{18}H_{32}O_2$), hypogaeic acid ($C_{16}H_{30}O_2$), or any other member of a considerable series of fatty acids, minus the acid ion H. The R radicals may be all alike or different. When digested, fats break up into glycerin and the fatty acid or acids. The fats contain a notably small proportion of oxygen.

The *lecithins* are substances allied to the fats in their constitution, containing phosphoric acid and cholin in place of one of the fatty acid radicals, R. They are very widely distributed in plants, and probably play an important rôle in the protoplasm, but just what is not known at present. It may be that they determine what substances may pass through the membranes; and it may be also that they are connected with the formation of chlorophyll.

Amides. — The name is here used loosely and not in its strict chemical sense for a group of substances of which none are popularly known. For convenience, they may be distinguished as nitrogenous compounds

intermediate between carbohydrates and proteins. On the one hand, they are derivatives of proteins, among whose decomposition products various amino-acids always figure. On the other hand, they are derivatives of the carbohydrates and their allies, from which, with proper additions, they are readily formed. In addition to the carbon, hydrogen, and oxygen of carbohydrates, they contain nitrogen, always combined with hydrogen as a definite radical, NH_2, known as the amide radical. It may replace an H or OH group in the various carbohydrates and their allied acids, converting them by this slight change into quite different substances.

Thus, either acetic acid, $CH_3—COOH$, or glycolic acid, $CH_2OH—COOH$, becomes amino-acetic acid (glycin), $CH_2(NH_2)—COOH$, by the substitution of the amide radical NH_2 for hydrogen (H) or hydroxyl (OH), respectively. Glucose, $COH—CHOH—CHOH—CHOH—CHOH—CH_2OH$, becomes glucosamin, $COH—CH(NH_2)—CHOH—CHOH—CHOH—CH_2OH$, by a like substitution. On the other hand, some of the constant decomposition products of the more complex proteins are glycin (*ante*); leucin, $\begin{matrix}CH_3\\ \\CH_3\end{matrix}\!\!>\!CH—CH_2—CH(NH_2)—COOH$; tyrosin, $OH—C\!<\!\begin{matrix}HC—CH\\ \\HC{=}CH\end{matrix}\!\!>\!C—CH_2—CH(NH_2)—COOH$; asparagin, $CO(NH_2)—CH(NH_2)—CH_2—COOH$; in all of which the amide radical has replaced H or OH of an allied substance.

Proteins. — Proteins are the substances which compose the larger part of the cytoplasm; protein foods, therefore, are those which can be most directly used for nourishment, and so represent the end of food making. To define proteins is quite impossible; they are so numerous and so varied that scarcely any characteristic is universal. Within this huge group are included some substances which are relatively simple, and others whose complexity defies all analysis. Even the simplest are scarcely known chemically, the actual knowledge permitting only theories of their construction. It has been possible in most cases to determine only the percentage composition, which with a study of the decomposition products sometimes permits the establishment of an empirical formula. The more complex proteins contain sulphur, and some have also phosphorus in addition to the carbon, hydrogen, oxygen, and nitrogen of amides, with traces of ash, which may or may not be structurally a part of the protein. One nearly pure protein is familiarly known, the albumin or "white" of eggs; perhaps the best known plant protein is the one longest known, the gluten of wheat grains.

To illustrate the complexity of these substances and, as well, the uncertainty regarding their composition, the following formulas, though hardly more than guesses, are quoted. A crystalline vitellin from squash: $C_{292}H_{481}N_{90}O_{83}S_2$. An albumin: $C_{720}H_{1134}N_{218}O_{248}S_5$. Haemoglobin (of the blood): $C_{712}H_{1130}N_{214}O_{245}FeS_2$; the same, another guess, $C_{600}H_{960}N_{154}O_{179}FeS_3$.

The most familiar physical characteristic of many proteins is that they coagulate; heat, prolonged shaking, the action of acids, alcohol, salts, etc., cause the protein to change from a liquid or semi-liquid form to a firmer "clot," which by pressure can be separated into a fluid and a more solid portion. The coagulation of white of egg by heat, of milk on souring, and of the fibrin of blood on contact with a vessel are familiar examples. Ordinarily the coagulum is insoluble in water. But the neutral salts act differently, producing a soluble clot. Advantage is taken of this fact to separate various mixed proteins and purify them partially for analysis by "salting out." Other physical peculiarities are their high resistance to the electric current, their large molecular weight (probably 15,000 and more in many cases) and hence slow diffusibility, so slow usually as to be negligible.

Some proteins crystallize, but most do not. When first discovered such crystals were called "crystalloids," because it was not believed that true crystals could be formed by organic matter. They are regularly present in the protein grains of the Brazil nut, castor bean, etc. (fig. 49).

Plant foods again. — Plant foods, then, are specifically these complex organic compounds — not the simple inorganic substances out of which green plants alone can make food. This is practically implied in the terms proposed by authors who reject this use of the term *food*, and used frequently to distinguish plants as to their mode of nutrition, viz. *autotrophic*, or self-nourishing, plants, and *heterotrophic* plants. The obvious objection to these two terms, if they are anything more than convenient and figurative ones, is that only some parts of most so-called autotrophic plants are strictly self-nourishing. Only the plants whose every cell contains chlorophyll are actually autotrophic. If the term be used in the wide sense, green plants are not merely self-nourishing — they nourish all living things.

Kinds of food needed. — However, there is a wide difference among plants as to the kind of food that they require. The known variety is so great that it is impracticable to state it in detail here, and only a small number of plants, chiefly fungi, have been carefully studied in

this respect. Some thrive best on comparatively simple compounds; others require the most complex proteins. Some flourish on material which is useless or even highly injurious to others. The proverb, "what is one man's meat is another man's poison," is quite applicable to plants. Among the lowest and simplest plants, the bacteria, there are some which live upon substances almost as simple as the food materials of higher plants; but they manage to secure energy in ways unknown to us, and build these substances into their bodies.

Food a source of energy. — After all, foods are of value to plants, as we conceive things, because they supply them with energy as well as with material. The energy income in this way is indeed the important feature. The green plant locks up in the food it constructs a fraction of the solar energy which reached it as light; and thus this energy becomes available to other organisms, since after further transformations of the foods they can release it by decomposition and apply it to other reactions.

Food and growth. — Because with our best appliances we are unable to know yet the real nature of nutrition, the use which a plant makes of food can be determined only by the extent to which it promotes growth and development of the body. The term *economic coefficient* has been used to express the ratio which the increase in the weight of a crop (say of a fungus) bears to a given quantity of a particular food. Manifestly there are other ways in which the plant uses a food besides incorporating it into the permanent structure of the body, and many complicated relations may be disturbed by too limited nutrition. Yet this economic coefficient expresses, in a crude way, the differences in the availability of foods for body building, and so impresses the fact that the processes of nutrition differ widely in different plants.

2. CHEMOSYNTHESIS

As was pointed out in an earlier paragraph, almost all organic foods are made by green plants; at least, all that is of economic importance as food for man and animals. Some of the lower forms of life, specific groups of bacteria, have the power to take CO_2 and H_2O and convert them into carbohydrates. As these forms do not need sunlight for their manufacture of food, they may well represent the primitive inhabitants of the earth; for they could live without other organic sources of food. They are independent, autotrophic bacteria.

Although such organisms do not use sunlight energy in making their

foods, they do require a source of energy. They obtain their energy, however, by oxidizing some particular chemical element. Because the energy used by these bacteria in synthesizing carbohydrates from CO_2 and water comes from chemical substances, this mode of synthesis is called *chemosynthesis*.

There are at least four or five groups of autotrophic, chemosynthetic bacteria. The nitrification bacteria, which oxidize ammonia to nitrite and nitrate, belong among the chemosynthetic organisms. They oxidize nitrogen to secure their energy. Certain sulphur bacteria utilize H_2S, and possibly other compounds containing reduced sulphur, as the source of energy. Still other forms oxidize hydrogen, and even iron and manganese may serve as sources of energy to the bacteria which have power to oxidize these elements from ferrous to ferric, or manganous to manganic state.

We have already considered the activities of nitrite and nitrate formers. We only need to add that there is release of chemical energy when NH_3 is oxidized to NO_2, or NO_2 to NO_3, just as when we oxidize carbon, in the form of coal, to CO_2. The bacteria carry on these processes of oxidation of nitrogen to nitrite and nitrate to secure the energy so set free. And they use a part of this energy to construct carbohydrate food from CO_2 and H_2O. While this food manufacture is not important in a direct way to mankind, the activities of these groups of organisms in converting the nitrogen of humus into nitrates which higher plants use as a source of nitrogen, are very important indirectly in the manufacture of all our foods.

Sulphur bacteria. — There are a number of groups of sulphur bacteria, as the purple bacteria, the beggiatoa, and thiobacillus. In general, the sulphur bacteria secure their sulphur from H_2S, or, more specifically, from the –SH radical. They are more abundant about sulphur springs than elsewhere, but they exist rather generally in soils where vegetable and animal matter is decaying.

Hydrogen sulphide is one of the products of protein decay, and it is oxidized to sulphur in the beggiatoa, for example. The beggiatoa belong to the endothiobacteria, those that deposit the sulphur in liquid form within their own bodies. The chemical reaction may be written thus:

$$4\,(-\mathrm{SH}) + \mathrm{O_2} \longrightarrow 2\,\mathrm{H_2O} + 2\,\mathrm{S_2}.$$

Well-nourished beggiatoa are often full of sulphur droplets produced within their bodies by the oxidation of the hydrogen sulphide. The

elemental sulphur, under appropriate conditions, is further oxidized to sulphuric acid, H_2SO_4, which then diffuses out into the environment. A very considerable amount of energy is set free during these oxidations, some of which appears as heat energy, but a part of the chemical energy is used to convert CO_2 and H_2O into carbohydrates.

The hydrogen bacteria. — These forms, like Hydrogenomonas, have the power to oxidize hydrogen to water. The reaction seems to be the same as in the ordinary explosion mixture of hydrogen and oxygen.

$$H_2 + O_2 \longrightarrow H_2O_2$$
$$H_2O_2 + H_2 \longrightarrow 2\ H_2O$$

We all know that the oxidation of hydrogen in the laboratory produces an intense heat. The energy yield is slow in the soil, and develops little heat; but the energy suffices for the manufacture of carbohydrates from CO_2 and H_2O. The hydrogen bacteria can, however, utilize carbohydrates when supplied to them as such. They do not have to depend on those produced by chemosynthesis.

Iron bacteria. — The iron and manganese bacteria also secure chemical energy by the changes already mentioned as produced by these organisms in the two metals named. Ferrous carbonate, ferrous sulphate, etc., are converted into ferric oxide, ferric hydroxide, ferric sulphate, with attendant release of chemical energy. The energy obtained can be used to manufacture carbohydrates, just as in the other cases.

While chemosynthetic bacteria occupy no very important place so far as the quantity of food made is concerned, we should not overlook their important contribution to the elemental cycles in nature. These organisms complete the cycles in the soil, converting the organic nitrogen, sulphur, and hydrogen into inorganic forms which can once more enter green plants, and take part in the great synthetic portions of the cycles which occur in living plants. These oxidative decay processes are necessary links in the natural cycles of the elements.

On the other hand, they are limited to rather special types of environment. They do not have universal distribution. With their equipment they were not designed to occupy the earth and to develop the food manufacturing activities upon which all animals and man depend. Yet when some plant invented chlorophyll, a universal environment became possible, for plants with chlorophyll could grow wherever light and water and appropriate temperatures occur.

3. PHOTOSYNTHESIS

The fundamental fact in the nutrition of all living things is the capacity of green plants to make certain complex organic compounds, carbohydrates namely, out of carbon dioxide and water, by the aid of light. This unique process is known as *photosynthesis*.

This process is one of the most important chemical processes in the world, and we owe to it not only all of our food supplies, but also our means of shelter, our clothing, our fuels, like wood, coal, oil, gas, lignite, and peat, most of which were formed by the photosynthetic activities of plants during past ages. Our industries and our commerce and transportation have been developed around the energy of coal and the distribution of plant products.

We depend upon green plants not only for all of these things, but also for certain chemical substances which we can obtain from no other source. Very few if any of the amino-acids are made in the animal body, so far as we know; and the vitamins, so valuable in growth processes and in the proper nutrition of man and other animals, are apparently made only by plants, mainly as a part of the photosynthetic processes occurring in green leaves.

As we have never been able to learn the secret of how a plant makes use of the sunlight energy, we are fully dependent on green plants for our sources of energy. There is at present no other known converter of sunlight energy into chemical energy, and chemical attempts along this line have failed to discover how the enormous energy of the sun can be artificially utilized in food manufacture. We must, therefore, learn, if possible, how to secure more energy through utilization of green plants. The time may come when we shall be totally dependent on green plants, for we are using coal, gas, oil, etc., at a very rapid rate. There is nothing in sight, as yet, to replace these when we have exhausted the supplies laid down in past geological ages.

The term used. — When the food of green plants was described as inorganic, this transformation of inorganic materials into carbohydrates, which was taken to be their incorporation into the body, was called assimilation, after the analogy of the transformations undergone by the food of animals. As the radical differences between the food making of a green plant and true assimilation in both plants and animals began to appear, an attempt was made to obviate the confusion by using the term *carbon assimilation*. These terms are still in common

use in other countries, but should gradually disappear.[1] Clearness demands the use of the distinctive term *photosynthesis* for the process that is peculiar to green plants, leaving the term *assimilation* to be applied to the same process in both plants and animals; namely, to the transformation of foods of all kinds into the actual living stuff.

As photosynthesis requires a supply of certain substances, which reappear in more elaborate form, and acts through certain structures, which require a supply of energy for doing the work, the making of carbohydrates may be described appropriately in terms of a manufacturing process. There are (1) the raw materials, (2) the laboratories, (3) the energy, (4) the products and the process.

(1) The Raw Materials

Carbon dioxide. — The raw materials needed have already been named, carbon dioxide and water. Carbon dioxide exists everywhere in the air, in the ratio of about 3 parts in 10,000, and its nearly uniform distribution is assured by the convection currents (winds) that stir the atmosphere. Only in the neighborhood of cities or other places where CO_2 is being produced in quantity is there temporarily an excess. By decomposition of rocks, volcanic production of CO_2, burning of fuel, decay of organic matter, and respiration of plants and animals, the supply of CO_2 is maintained, though great quantities are removed from the air by green plants. The amount is constant, so far as can be known historically, though there is geological evidence that in earlier periods of the earth's development CO_2 existed in much larger and also in smaller quantities than now, since enormous amounts have been fixed in beds of limestone, and later released by weathering.

The burning of fuel returns enormous amounts of CO_2 to the cycle of carbon in nature. For ages this carbon has been tied up in coal, oil, gas, etc., and now is being returned to the air. Nearly one and a half billion tons of coal are mined and burned each year, and hundreds of millions of gallons of gasoline and oil are consumed. Every ton of coal burned produces two and a half tons of carbon dioxide in the air. Even with this enormous production of CO_2 from ancient supplies of carbon, the CO_2 content of the air is increased only about a sixth of one per cent of the amount now present each year, too small an amount to be measured. It would require over 600 years to double the carbon dioxide content of the air by coal combustion.

[1] For example, a recent hybrid is "photosynthetic carbon-assimilation"!

CO_2 near the ground. — On quiet days there is a layer of air near the ground where the proportion may rise much higher (10 to 12 times as much), owing to the diffusion of CO_2 from the soil, where it is being evolved by the decomposition of organic matter through the agency of bacteria, etc. Perhaps turf-forming and rosette plants profit from the lowly position of their leaves, since the more CO_2 in the air, within limits, the more can enter them and be used for food making.

CO_2 in water. — In the water of quiet pools and lakes, as well as in slow streams, the amount of CO_2 dissolved is much greater than in the air. It is produced by the host of organisms living in the waters and by decay, and is also dissolved from the air. The oceans themselves are great reservoirs of CO_2; there is about 50 cc. of carbon dioxide in every liter of sea water. The total carbon dioxide content of the oceans is actually greater than that of the whole atmosphere of the earth. As CO_2 is very soluble in water (up to volume for volume at ordinary temperatures), it may thus accumulate to 25 or even 100 times as much as in the air. This puts water plants in a very advantageous position so far as a supply of CO_2 is concerned.

Admission of CO_2. — Of course in all plants that present an uncutinized (and consequently a wet) surface to the air, the CO_2 enters directly at the surface; in fact it can enter, in proportion, wherever water can evaporate. As the cuticular evaporation in most of the higher plants is small, the quantity of CO_2 entering through the epidermis is trifling. Into some epiphytic seed plants which have no stomata (*e.g. Tillandsia*), the leaves of mosses, the thallus of liverworts, etc., CO_2 enters directly.

The supply for the great majority of the larger land plants, however, passes through the stomata. These openings are ample to admit not only what is necessary, but five or six times more than actually passes through them in nature.

It has been shown that CO_2 will diffuse through a multiperforate partition, placed over some ready solvent like sodium hydroxide, as freely as it would enter the solvent were the partition absent, provided the perforations are not farther apart than ten times their diameter. The epidermis is like such a multiperforate partition in which the area of the openings is scarcely more than 1 per cent of the total surface. But the CO_2 dissolves so readily in the wet cell walls bounding the intercellular spaces that its pressure in the internal passages is usually low; so it may traverse the stomata as rapidly as is permitted by the gradient of pressure. The speed of the molecules is found to

be greatly accelerated as they swirl through the narrow passage of a stoma; in fact, they traverse it at a speed about 50 times as great as when diffusing freely into sodium hydroxide.[1]

Even when the orifice of the stoma is partly closed, though this reduces proportionately the amount of gas passing, the supply of CO_2 is not likely to fall below the maximum that can be used. As in good light the stomata are usually more than half opened, even though the evaporation is excessive, an adequate supply of CO_2 is thus assured, so far as admission to the aërating system is concerned.

Deficiency in CO_2. — As a matter of fact, however, the supply of CO_2 is often less than could be utilized by the chloroplasts. This is shown by the fact that photosynthesis is increased when, in good light, the amount of CO_2 in the air around the plant is artificially increased. The increase may go to a hundredfold or more with positive benefit, at least so far as brief experiments show. Any increase of CO_2 in the air means increased pressure of CO_2 in the aërating passages; and this means the solution of more CO_2 in the wet walls, and consequently faster diffusion toward the chloroplasts, where the CO_2 is actually utilized. Here, indeed, is the point at which the normal pressure of CO_2 usually limits the process of photosynthesis. The main-line transportation through stomata and intercellular spaces is adequate, but the switching facilities in the terminal yards (from cell wall to chloroplast) are not; hence when otherwise capable of operating to full capacity, the laboratories are hindered by the impossibility of securing enough of this raw material. There are other factors which may limit the output, to be discussed later; but the shortage of CO_2 due to low diffusion pressure is the commonest.

Water. — Water, the other of the raw materials, is never lacking when plants are active. Its source for most land plants is the soil water that enters through the roots. The little that may enter *via* the leaves (comparable with the amount leaving in the same time by cuticular evaporation, p. 56) is practically negligible in most cases. Only in mosses, liverworts, and a few epiphytes, *i.e.* plants with practically uncutinized surfaces, may it freely enter aërial parts. In many cases there are special structures that hold water until it can enter.

Relation of CO_2 and H_2O. — The carbon dioxide and water enter into a double relation. In part, the CO_2 is merely dissolved in the water; in part the two form a loose chemical combination, carbonic

[1] Brown, H., and Escombe, F. *Trans. Roy. Soc.* Lon. B. **193**: 223–292. 1900.

acid, H_2CO_3. This three-phase system, solute, solvent, compound, is in equilibrium, and if the amount of any member is altered, corresponding changes take place in others and equilibrium is again reached.

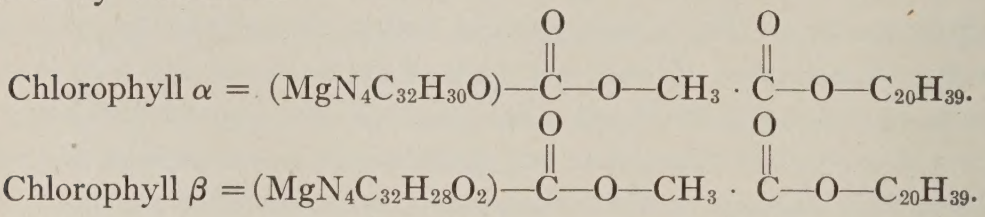
(2) The Laboratories

Chloroplasts. — The laboratories in which photosynthesis proceeds are the chloroplasts. These are organs of various form and size, found only in superficial parenchyma cells, *chlorenchyma*, of stems and foliage. (For a discussion of this tissue and its relations to external agents, see Volume III, *Ecology*.) The chloroplasts are embedded in the cytoplasm just within the ectoplast and marked by their green color. In a few algae (especially the Conjugales, p. 37, Volume I, *Morphology*) they have various and sometimes fantastic forms, but in almost all the higher plants they are shaped like a bun or a thick round cake; that is, two diameters are nearly equal, and the other is shorter, with the convexity greater on one face than the other (see fig. 1, p. 1). Their form is subject to change from internal causes, and in moving about with the cytoplasm they are easily distorted by pressure, showing that they are of a soft, elastic, and semi-fluid consistency.

Pigment and stroma. — In fact, the body or *stroma* of the chloroplasts seems to be like the cytoplasm, but dyed by the green pigment. The precise relation between the pigment and the stroma has not been satisfactorily made out, even in the killed chloroplast, and in the live unaltered choloroplasts it can only be conjectured. In some cases, when the pigment has been dissolved out by alcohol, the stroma (of course coagulated by the alcohol) presents a spongy appearance, and it has been inferred that the meshes of the sponge throughout were occupied by pigment. In others, especially in the larger chloroplasts which can be sectioned, the pigment seems to be restricted to a spongy shell of measurable thickness at the surface, while the interior is colorless. It seems probable that the cholorophyll is either adsorbed on the surface of colloidal elements of the stroma, or combined in loose chemical union with proteins of the stroma.

Pigments. — Four pigments are commonly associated together in the chloroplasts of plants. Two of these are green, constituting the genuine chlorophylls. They differ only slightly in chemical composition and have been designated by Willstätter, who isolated them, as *chlorophyll* α and chlorophyll β. The other two pigments are yellow, and are known as *carotin* and *xanthophyll*.

Chemically, the two green pigments are esters, formed by the combination of a tricarboxylic acid with two alcohols, methyl alcohol and phytol, which are seen as —O—CH_3 and —O—$C_{20}H_{39}$ in the formulas. The formulas now generally accepted for the two chlorophylls are those given by Wilstätter.



Chlorophyll α = $(MgN_4C_{32}H_{30}O)$—C(=O)—O—CH_3 · C(=O)—O—$C_{20}H_{39}$.

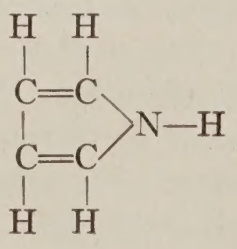
Chlorophyll β = $(MgN_4C_{32}H_{28}O_2)$—C(=O)—O—CH_3 · C(=O)—O—$C_{20}H_{39}$.

They differ from one another chemically only in the amount of hydrogen and oxygen in the nucleus of the molecule. Chlorophyll β has two less hydrogen atoms and one more oxygen atom than chlorophyll α. Chlorophyll α is usually much more abundant in leaves than the chlorophyll β, about three times as much. The two chlorophylls also differ some in color, solubility, melting point, absorption spectrum, and fluorescence.

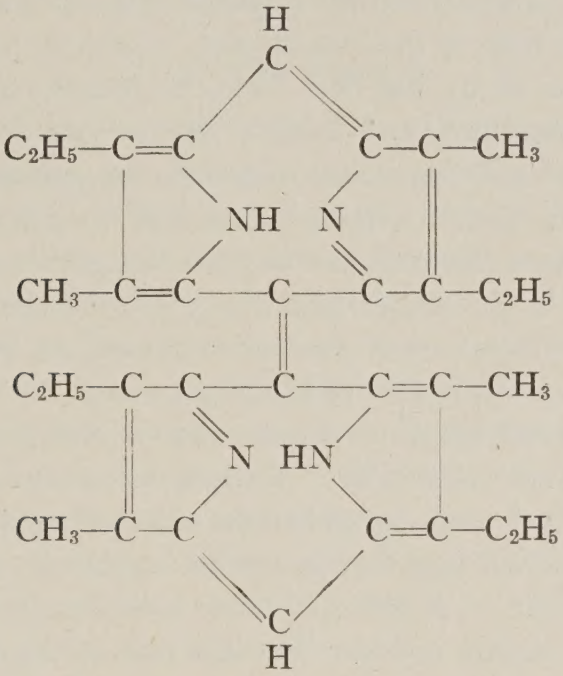
It should be noted that Mg is the only metallic element in chlorophyll, and that the ashes of pure chlorophyll α and β is pure magnesium oxide. There is no iron in chlorophyll, although iron is needed for the development of the green pigments, as was pointed out in an earlier chapter.

The red coloring matter of blood, haemoglobin, yields decomposition products very similar to those yielded when chlorophyll is decomposed. This fact indicates a structural similarity between chlorophyll and haemoglobin. It seems that the haemin of the blood pigment and the main portion of the cholorophyll molecule are derivatives of a compound known as *aetioporphyrin*. But in haemin, the metallic element is iron, instead of magnesium.

The formulas suggested for such decomposition products of chlorophyll as aetiophyllin and aetioporphyrin, and the haemin and haemoporphyrin from haemoglobin, indicate that they are made up of substituted pyrrol rings, four to each molecule. Pyrrol itself is a cyclic compound having four carbons and a nitrogen atom in the ring, thus:



On examination of the formula of aetioporphyrin, we find four pyrrol rings represented, but some of the hydrogens attached to the carbons have been replaced by alkyl groups, such as CH_3, or C_2H_5. The formula of aetioporphyrin is shown here, to give an idea of the possible arrangement of these four substituted pyrrol rings in the molecule.



Aetioporpoyrin. — As this compound contains about the same number of carbons, hydrogens, and nitrogens as the main part of the chlorophyll molecule, it may be that the chlorophyll molecule has much the same arrangement. The aetioporphyrin is $C_{32}H_{36}N_4$, while chlorophyll α has $C_{32}H_{30}N_4$ in this part of the molecule. The Mg of the chlorophyll molecule is pictured by Willstätter as united to the N atoms, displacing some of the hydrogens attached to the nitrogen. This is probably not the correct arrangement, but we do not yet know just where the magnesium is attached.

May it not be possible that the chlorophyll in the food eaten by animals furnishes in part the building materials from which the animal constructs its haemoglobin? This may account for the similarity between the chlorophyll on the one hand, and haemoglobin on the other, when we study the decomposition products of the two pigments.

In the autumn, when chlorophyll is disappearing from the leaves, the yellow pigments remain, giving the golden colors to the foliage.

Some of the decomposition products may share in the production of the red colors, anthocyans, which are usually dissolved in the cell sap of such cells as contain them. The yellow colors remain in the leaf cells. But autumn colorations are not yet fully understood.

The decomposition of chlorophyll seems to be an oxidation process,[1] and it has been found possible to hasten chlorophyll decomposition artificially. Ethylene in the atmosphere, 1 part to 1000, or as dilute as 1 part to 50000 of air, has been found to blanch celery fairly well,[2] and oranges, tangerines, and lemons[3] are prepared for the market sometimes by precoloring them through the agency of ethylene. These citrus fruits ripen internally before they are ripe looking outside. By precoloring them, the fruit can be marketed earlier, and the process of yellowing can be put under control. The ethylene has been found to increase the respiration of the parts treated, as measured by the amount of carbon dioxide set free in a given time.[4]

Carotin and xanthophyll. — These two yellow pigments are also very closely related chemically. Carotin is an unsaturated hydrocarbon; that is, it is made up of carbon and hydrogen only, and some of the carbons are held together by double bonds between the carbons. The formula is $C_{40}H_{56}$. Xanthophyll has a similar formula, $C_{40}H_{56}O_2$, which looks like carotin dioxide; but it is not an oxidation product of carotin, so far as we know. These pigments are widely distributed in nature, and xanthophyll is somewhat more abundant usually than the carotin. The functions of these compounds, if they have any, are not definitely known. It was thought at one time that the yellow pigments were closely associated with vitamin activity, and it is true that vitamins are more abundant in most yellow foods than in others. Yellow corn is superior to white corn. Yellow butter is richer in vitamin than the pale butter of winter time. But it has not been possible to prove a relationship between these pigments and vitamin activity. They do give the yellow color to butter, yolks of eggs, skins

[1] Wager, H. The action of light on chlorophyll. *Proc. Roy. Soc.* Lond. B. **87** : 386–407. 1914.

[2] Harvey, R. B. Blanching celery. Minn. *Agr. Exp. Sta.* Bull. 222. 1925.

[3] Denny, F. E. Hastening the coloration of lemons. *Jour. Agr. Res.* **27** : 757–769. 1924.

[4] Denny, F. E. Effect of ethylene upon respiration of lemons. *Bot. Gaz.* **77** : 322–329. 1924.

Regeimbol, L. O., Vacha, G. A., and Harvey, R. B. The effect of ethylene on the respiration of bananas during ripening. *Plant Physiol.* **2** : 357–359. 1927.

and fats of animals, as well as the yellow colors of leaves, flowers, and possibly some of the yellow fruit colors. In yellow apples, however, the yellow color is due to *quercitrin*, one of the flavones. The presence of carotin and xanthophyll in animal organs is to be traced to the food the animal eats. The carotin of milk is the same carotin that was in the grass and corn eaten by the cow.

(3) The Energy

Light. — While the intricate chemical relations of chlorophyll are only partially known, one of its physical features is known to be of the greatest importance. That is its capacity to absorb radiant energy. When the radiant energy coming from the sun is passed through prisms of rock salt, glass, or other appropriate media, or is reflected from a minutely striate surface, the various wave lengths are unequally refracted or reflected, so that the physiological and other effects of energy of different wave lengths can be studied. Certain of these wave lengths (if they were sound waves one might say about 1 octave out of 11) affect our eyes, and this physiological effect is what we know as light. By a figure of speech the cause is likewise so named, and the waves themselves are called "light." But they differ only in length and frequency from the much greater number, both longer and shorter, slower and faster, which we cannot perceive with our eyes. Other physiological effects, such as inflammation of the skin and the development of pigment ("sunburn"), are produced by light waves. On the plant, likewise, waves of different lengths produce different effects according as certain parts are attuned to them.

Absorption spectrum. — The chlorophyll is so constituted that it can absorb waves of certain lengths, all falling within the range of our vision. On the plant this energy cannot produce the effect that it does on our eyes, and hence for the plant it is "light" only by a convenient figure of speech. There are seven separated groups of waves whose absorption is more or less complete. When we look at a spectrum of sunlight, *i.e.* a narrow bar of light dispersed into a band of different wave lengths, each group of waves produces its appropriate effect and we see a band of blending colors, dark red at one end, running through red, orange, yellow, green, blue, indigo, violet, and ending in the darkest violet. On interposing a leaf in the path of the light, there appear across the spectrum dark strips due to the partial or complete stoppage of the energy. Similar *absorption bands*, slightly displaced,

are seen by using in the same way an alcoholic solution of chlorophyll (fig. 33).

These absorption bands are as follows: 1, in the red a wide black one, its wave lengths (λ) being 670–635 mμ[1]; 2, a narrower and less intense one in the orange, λ = 622–597 mμ; 3, in the yellow, a band much lighter than 2, and shading out on the sides, λ = 587–565 mμ; 4, a faint band in the green, not always to be seen, and probably due to decomposition products, λ = 544–530 mμ. Ordinarily the other three blend into one, and there are no visible waves

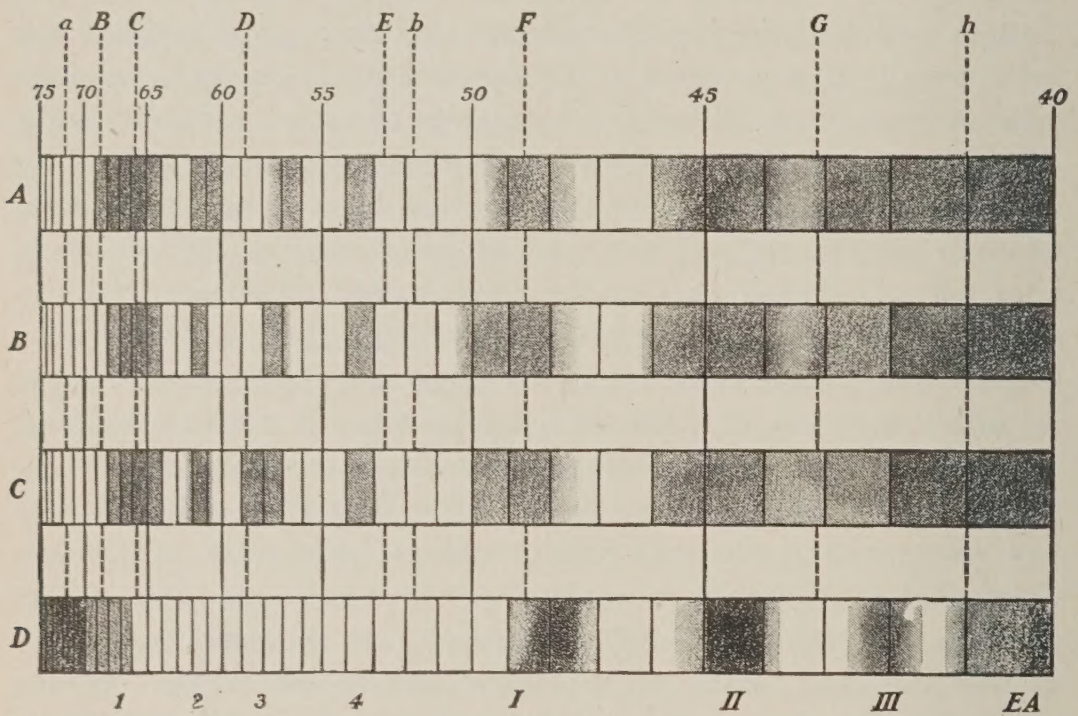


FIG. 33. — Absorption spectra: *A*, chlorophyll of *Allium ursinum* in alcohol; *B*, chlorophyll of English ivy (*Hedera Helix*) in alcohol; *C*, chlorophyll of *Oscillatoria* in alcohol; *D*, carotin. 1, 2, 3, 4, absorption bands of chlorophyllin; *I*, *II*, *III*, absorption bands of carotin; *EA*, end absorption. The lettered broken lines mark the position of the principal absorption lines of the solar spectrum (Fraunhofer lines); the numbered solid lines form a scale from which wave lengths (λ) in millionths of a millimeter may be found by adding a cipher; note the increasing dispersion from left (red) to right (violet). — After KOHL.

left beyond the blue (λ = 495–420). By very careful manipulation, using dilute solutions instead of a leaf, they can be distinguished, their limits not being sharply marked. Willstätter gives the absorption bands for carotin solution in a 10 mm. thick layer, as λ = 492–276, λ = 459–445, and λ = 419 and beyond, for the end absorption. The bands 1–3, and possibly 4, belong to the chlorophylls, while the indefinite three, *I–III*, belong to carotin and xanthophyll. These three are much better seen in the absorption spectrum of the yellow pigments alone (fig. 33, *D*).

Fluorescence. — Chlorophyll has another physical character, which it shares with some other dyes; it is fluorescent not only in solution, but also

[1] The exact location of the bands varies. 1 mμ = 0.000001 mm.

in the living plant. When a strong solution in alcohol is held between the eye and the light, the color is a vivid green; but if examined by bright reflected light, it appears deep blood-red. While this is a useful recognition mark, the physiological significance of fluorescence, if any, cannot be explained.

Fluorescence is explained as light emitted from the solution by the rapid vibration of the chlorophyll particles. See Kimball's *College Physics* for a discussion of the nature of fluorescence.

The absorbed energy. — The energy that drives the machinery is derived from light, for if a green plant be kept in darkness, it is entirely unable to make any carbohydrates. Furthermore, it is only the chloroplast directly illuminated that receives this energy. A lighted portion of a leaf cannot communicate the energy to a darkened area. If a portion of a leaf be covered with an opaque plate, while CO_2 is allowed free access, the rest of the leaf may show evidence of active photosynthesis, but the darkened area shows none. Moreover, it is the energy absorbed by the chlorophyll that does the work.

The following experiment shows this: A plant was kept in the dark until its leaves showed no trace of starch. Then on a sunny day a spectrum of sunlight, as bright as possible, was cast on a leaf and kept steadily in the same place for some hours. Thus the chlorophyll could absorb energy only in those regions along the band of light where fell the waves of lengths that it can stop; on the leaf these regions of course corresponded in position to the absorption bands before described. If, therefore, the leaf works with the absorbed energy, photosynthesis can occur only in these strips and not elsewhere. After the exposure, on testing the leaf for starch (the accumulation of which is a mark of active photosynthesis), it was found in abundance where lay absorption band 1 (fig. 33), and scantily in others; but it was wholly lacking in other parts of the spectrum.

This is what would be expected; but there was once an idea that chlorophyll acted merely as a screen, shading the protoplasm from harmful rays of light; and that the protoplasm could work properly only behind such a screen. Although the protoplasm must play some part in photosynthesis, it seems probable that the chlorophyll does not serve as a screen for protection. It is possibly light transformed to electricity that reduces the H_2CO_3 to formaldehyde (see p. 139), which then condenses into more complex carbohydrates.

Exposure to light. — Plainly the light which has passed through a chloroplast is unlike that which has not; and the more chloroplasts it passes through, the more complete is the absorption of effective waves. The upper cells of a leaf, therefore, are in a more favorable position

with respect to light than the lower, especially in weak or diffuse light; but if the stomata are only on the under surface, as they often are, the lower cells are more favorably placed with respect to CO_2; and the more so as the looser arrangement of these cells permits freer diffusion. The very structure of the leaf is in large measure a response to these different factors, and so perhaps the advantages and disadvantages balance one another. A leaf which is directly shaded by another is obviously in a decidedly disadvantageous situation; and we observe various arrangements and positions that reduce shading. These result in leaf mosaics of various kinds (see *Ecology*). A plant that grows in shade is different from the same species grown in the sun; indeed shade plants have peculiarities which depend in large part on the difference in the illumination (see *Ecology*).

Energy obtained. — An ordinary thin leaf reflects and absorbs 40–70 per cent of the sunlight which falls upon it; but of diffuse light it absorbs about 95 per cent. The chlorophyll itself seems to absorb something like 20–30 per cent, but of this only a small part can be used for photosynthesis and so stored as potential energy in the carbohydrate made. That amount is variously estimated from 0.5 to 3 per cent. The balance is free to heat the leaf, whose internal temperature in the sun sometimes rises 10–15° above that of the air. This surplus heat, of course, is partly transferred to the air adjacent by thermal emissivity, but the greater part becomes latent in the water, whose vaporization is accelerated thereby. This is the so-called "chlorovaporization" (see p. 73).

Deficiency in light. — It will be evident from the foregoing that in nature light is seldom lacking to drive the machinery rapidly enough to dispose of all available CO_2. Yet it may be reduced to an intensity at which light, instead of the small supply of CO_2, limits the output. For example, some plants are so situated that they get only 2 per cent of the total sunlight in the vicinity. From the point at which the effective energy of the light absorbed is just equal to disposing of the available CO_2, whether this is greater than natural or not, lessening the intensity of the light results in a proportional diminution of the amount of the product.

Efficiency. — It will be further evident that the plant is a very inefficient machine, considering the relation of energy received to the energy stored in the product. A steam engine which delivers as mechanical power less than 10 per cent of the energy of the fuel consumed

under the boilers is fit for the scrap heap, and the best types are delivering about 25 per cent. Contrast this with the 0.5–3 per cent of the plant economy. Yet in spite of this relative inefficiency, the total product is enormous and invaluable, because of the limitless store of energy pouring upon the earth constantly from the sun, beside which the artificially released energy of fuel is absolutely a negligible quantity. Abbot has estimated that the earth receives from the sun each year energy equal to the burning of 4×10^{23} tons of anthracite coal.

[1] The solar energy received by the earth in a *second* is represented by 250×10^{15} calories. The coal consumed in the whole world in a *year*, reported in 1920 as about 1300 million metric tons,[1] represents 10.4×10^{15} calories. The plant can afford, so to speak, to be inefficient.

Source of light. — The source of light is quite a matter of indifference. In nature, of course, the primary source, the sun, is alone to be considered, since the light of even the full moon (only $\frac{1}{600000}$ that of the sun) is too weak to effect photosynthesis to a measurable extent. Various secondary sources may be used in experiments, some electric lamps and the incandescent mantles (with gas) giving light of sufficient intensity when near the plants. Attempts to "force" plants, by enabling them to make food by night with electric arc illumination, have been successful with certain sorts, showing that there is no need for rest at night, and that a greater supply of food permits more rapid development; but there will be no incentive for commercial application of this result until the cost of electric energy is vastly less than now.

Temperature. — A suitable temperature has usually been considered merely a condition of photosynthesis, and not a source of energy for the process. This is evidence that our knowledge of the energy relations of this process is vague, and that the matter needs investigation. At present, however, it is not possible to describe in terms of energy the effect of heat upon photosynthesis, so we must be content with a brief statement on temperature as a condition.

Experiments show that even at temperatures considerably below 0° C. some plants can make carbohydrates; thus it is claimed by Jumelle that *Picea excelsa* still carried on photosynthesis at −35° and some alpine flowering plants begin photosynthesis at about −15° C., and the algae of arctic waters must be kept at about 0° C. for long periods at a

[1] The metric ton about equals the English "long" ton, 2200 lbs.

time. Yet for most plants such a low temperature practically stops photosynthesis; while even at several degrees higher it may be the limiting factor, less food being made than the CO_2 and light would permit. Likewise in direct sunlight the temperature may rise so high in the interior of a leaf as to retard photosynthesis;[1] and in tropical deserts, where the heat of the air itself may run to 45° C., it is probable that photosynthesis is reduced thereby.

The influence of temperature on the rate of photosynthesis has been the subject of many investigations. At ordinary temperatures the value of Q_{10}, the temperature coefficient, for photosynthesis is about 2.1; that is, a rise of ten degrees about doubles the rates of the process if no limiting factors like deficiency of CO_2 or low light intensity intervene. This value is close to that expected from Van't Hoff's rule. But at higher temperatures photosynthesis falls off with time, probably due to injury of the protoplasm, or to inactivation of enzymes concerned in the process. This falling off in rate with time at high temperatures is called the Blackman "time factor," because Blackman[2] first emphasized it as a factor in quantitative studies of photosynthesis.

At high illumination intensities a rise of 10° C. causes a doubling of the rate of synthesis; but at low light intensities the 10° C. rise has little effect. It is believed that photosynthesis involves two reactions at least, a photochemical stage which determines the rate at low light intensities, and an ordinary chemical reaction that determines the rate at high light intensities. The first of these reactions has a low value for Q_{10}, the second follows the Van't Hoff rule approximately in its temperature relations.

(4) The Products and the Process

The products. — The first product of photosynthesis is now believed to be the simplest of the aldehydes, formaldehyde. The product of later synthesis which is most general and has been longest known is starch. The fact that it is so generally present and that it is so universally used as evidence of photosynthesis because it can be so easily detected, tend to confirm the common impression that starch is *the* product of photosynthesis. But there are many plants in which starch is either not formed at all, as in the onion, or appears only under

[1] But these heating effects of direct sun are compensated in a measure by evaporation.

[2] Blackman, F. F., and Matthaei, Gabriella L. C., Experimental researches on vegetable assimilation and respiration. IV. A quantitative study of carbon dioxide assimilation and leaf temperature in natural illumination. *Proc. Roy. Soc.* Lond. B. **76** : 402–460. 1905.

exceptional conditions, and in no plants is it the exclusive product. Thus, in most fungi no starch is formed when they are fed on carbohydrates; in the kelps fucosan takes its place, and in many monocotyledons, oil; while even in the plants which produce starch abundantly, much of the earlier product is diverted into amides and possibly other nitrogenous compounds.

In any event starch is a secondary product, and represents the surplus in the manufacture of primary carbohydrates over immediate use, removal, transformation into amides, etc. That starch does not appear under certain conditions, in a leaf in which it is usually formed, is no evidence, therefore, that no photosynthesis has occurred, but only that it has not gone on at a rate rapid enough to yield enough excess to appear as starch.

It is generally believed that glucose or dextrose is the first carbohydrate which can be recognized in the leaf, and dextrose has sometimes been called the photosynthate. From dextrose by enol formation can be derived fructose and mannose, since these three sugars have the same enol structures. Cane sugar is produced by condensation of dextrose and levulose (fructose). By condensation of dextrose alone, starch and cellulose are formed; and by condensation of levulose alone, inulin arises. In all cases, condensation involves the loss of water, as the molecules of simpler sugars unite to form the more complex carbohydrates. These condensations are controlled by enzymes, probably the same enzymes that digest the reserve carbohydrates when the reserve foods are utilized.

The pentose or five carbon sugars in all probability arise from the hexoses by the oxidation of one of the carbons in the hexose chain, although some molecules of pentose may form directly form five formaldehyde groups, just as the hexoses are supposed to arise from six such groups, as will be shown a little later in discussing the process of photosynthesis.

In addition to providing the materials for building all of the carbohydrates, including cellulose, the hexoses furnish the hydrogen and carbon building materials for the construction of the fats and proteins. They enter into the various glucosides, some of which are colored and form the interesting soluble anthocyanin (blue and red) sap pigments. Dextrose is also the principal respiratory form of carbohydrate, so that whether we consider the synthetic or catabolic processes of plant life, dextrose seems to be the key sugar of metabolism.

Amount of product. — A method of estimating the amount of photosynthesis under various conditions is based upon the relative weight of equal, but necessarily small, areas of leaves, taken at the beginning and end of the experimental time, allowances being made for migration[1] and use by data from other experiments. The results at best cannot be exact, and the introduction and multiplication of small initial errors make the calculations based on these data quite unreliable.[2]

When accurate data for photosynthesis are needed, the only reliable method is to determine the amount of CO_2 used. This requires rather complicated apparatus, skillful manipulation, and accurate gas analysis. This method is obviously independent of the products and their use or migration.

The best estimates as to the amount of photosynthesis carried on by thin-leaved plants are given in the following table:

CARBOHYDRATE MADE IN 1 HR. BY 1 SQ. M. OF LEAF SURFACE

NAME OF PLANT	CONDITION OF LEAF	LIGHT	TEMP. °C.	CO_2 USED, CC.	CO_2 USED MG.	CARB. MADE, MG.
1. Helianthus annuus .	attached	diffuse	21.2	312.6	612	392
2. Helianthus annuus .	detached	diffuse	19.0	439.9	862	551
3. Helianthus annuus .	detached	strong to diffuse	26.8	385.3	755	483
4. Helianthus annuus .	attached	bright sun	47.1	21.9	43	27
5. Tropaeolum majus .	detached	diffuse	21.7	158.3	310	198
6. Tropaeolum majus .	detached	diffuse	25.9	243.7	487	305
7. Catalpa bignonioides	detached	interm. sun	20.0	373.2	737	468
8. Petasites albus . .	detached	interm. sun	17.0	208.4	408	261
9. Polygonum Weyrichii	detached	. . . .	21.0	473.2	927	593
10. Prunus Laurocerasus	detached	. . . .	10.0	. . .	. . .	281
11. Prunus Laurocerasus	detached	. . . .	37.5	. . .	. . .	810
12. Helianthus annuus .	detached	. . . .	19.0	. . .	. . .	569
13. Helianthus annuus .	detached	. . . .	29.0	. . .	. . .	650
14. Helianthus annuus .	detached	. . . .	35.0	. . .	. . .	730

Nos. 1–9, after BROWN and ESCOMBE,[3] in part recalculated; nos. 10–14, after BLACKMAN and MATTHAEI,[4] especially intended to show the effects of temperature on photosynthesis. An effect of excessive temperatures is to be seen also in no. 4.

[1] Or this may be rendered impossible by severing the leaf from the plant.

[2] The results obtained by this method are two to three times as large as those in the table here presented.

[3] Brown, H. T., and Escombe, F. Static diffusion of gases and liquids in relation to the assimilation of carbon and translocation in plants. *Phil. Trans. Roy. Soc.* Lond. B **193**: 223–291. 1900.

[4] *Loc. cit.* See reference 2, page 134.

Using such results as the basis of calculation, it would be easy to show how enormous a weight of food is made in a growing season by the foliage of meadows and forests. But unknown allowances must be made for leaves unfavorably situated or lacking in vigor, and such estimates are of little value except for their impressiveness. The value and volume of the annual crops of cultivated plants is even more impressive; and to this must be added in imagination the unknown but huge volume of wild vegetation, all dependent upon photosynthesis for at least 85 per cent of its dry substance.

The following are the approximate values of some of the more important crops of 1925 in the United States: corn, $1,950,000,000; wheat, oats, rye, and barley, $1,680,000,000; cotton, $1,460,000,000; hay, $1,400,000,000; potatoes, $600,000,000. Together the weight of these marketable products is something like 300,000,000 tons; and of course this is but a small fraction of the vegetation that produced them. In addition to the staple crops just named, whose aggregate value in 1925 was about $7,000,000,000, other farm crops add about one third more, being estimated at $2,000,000,000. Such are the values that plants annually produce in this country, chiefly from the air and water, by photosynthesis.

Process. — The process of photosynthesis has received much attention from botanists and chemists, but we are still not very sure of the exact steps in the process of building dextrose in the plant cell. In 1864 von Baeyer suggested that carbon dioxide was reduced to carbon monoxide, which then took up hydrogen to form formaldehyde, $CO + H_2 \longrightarrow H—\overset{\overset{O}{\|}}{C}—H$. Although this form of the theory was abandoned long ago, the idea that formaldehyde is the product of CO_2 reduction and the chemical substance from which the sugar, dextrose, is formed, has persisted. The only reason why this formaldehyde hypothesis was not firmly established was the inability of botanists and chemists to prove that formaldehyde is an intermediate product between carbonic acid, H_2CO_3, and sugar. Aldehyde can be found in small amounts in plants, but it is usually acetaldehyde, a product of respiration. The aldehydes are so similar in their reactions that it was very difficult to prove the presence of formaldehyde, or if found, to prove that it arose during photosynthesis as a part of that process, rather than in some other metabolic processes.

The very fact that we were unable to find free formaldehyde[1] readily

[1] Spoehr, H. A. The theories of photosynthesis in the light of some new facts. *Plant World* **19**: 1–16. 1916.

in leaves during photosynthesis was considered by some as favorable to the formaldehyde hypothesis. For this compound is very reactive, and may combine so quickly that it may not exist free in sufficient quantities to be easily isolated and identified. For instance, carbonic acid may unite right in the beginning with some of the protein constituents associated with chlorophyll, in what is called a carbamino reaction. This reaction is supposed to tie the $-\overset{\overset{O}{\|}}{C}-OH$ of the carbonic acid to the $-NH_2$ group of the protein, and from this carbamino compound, the forerunner of the sugars, formaldehyde, may be derived, without its ever existing free in the tissues.

We cannot consider all the complex theories that have been proposed, such as Willstätter and Stoll's chlorophyll-carbonic acid theory,[1] and Maquenne's[2] modification of it. These theories have no real facts to support them, but represent ingenious attempts to picture sugar manufacture in the green cell without free formaldehyde.

Recently the formaldehyde hypothesis has received some support in the discoveries of Klein and Werner,[3] who, using Neuberg's dimedon reaction, have been able to demonstrate that formaldehyde is produced during photosynthesis, and only then. Anaesthetics stopped the formation of formaldehyde almost immediately, but on removal of the anaesthetic, the process was resumed. As this work seems to be trustworthy, we can reasonably accept the formaldehyde theory of sugar formation in plants.

For our purposes, all that is necessary is to understand that carbonic acid undergoes reduction, with formaldehyde as the most probable intermediate product in the formation of the sugars. A simple picture of the process is desirable for students, even if we are not sure of the exact steps; and since formic acid and hydrogen peroxide have both been found as by-products of the reactions yielding the formaldehyde, the following steps are offered as a simple picture of the process.

[1] Willstätter, R., and Stoll, A. *Untersuchungen über die Assimilation der Kohlensäure.* Berlin. 1918.

[2] Maquenne, L. Sur la theorie de la synthese chlorophyllienne. *Compt. Rend. Acad. Sci.* Paris. **177**: 853–857. 1923.

[3] Klein, G., and Werner, O. Formaldehyd als Zwischenprodukt bei der Kohlensäureassimilation. *Biochem. Zeitschr.* **168**: 361–381. 1926.

The first step is the solution of carbon dioxide and its chemical union with water to form carbonic acid.

$$(1)\quad CO_2 + H_2O \longrightarrow HO{-}\overset{\overset{O}{\|}}{C}{-}OH$$

The second step may be pictured as a partial reduction of the carbonic acid, with water serving as the reducing agent.

$$(2)\quad HO{-}\overset{\overset{O}{\|}}{C}{-}OH + H_2O \longrightarrow H{-}\overset{\overset{O}{\|}}{C}{-}OH + H_2O_2$$

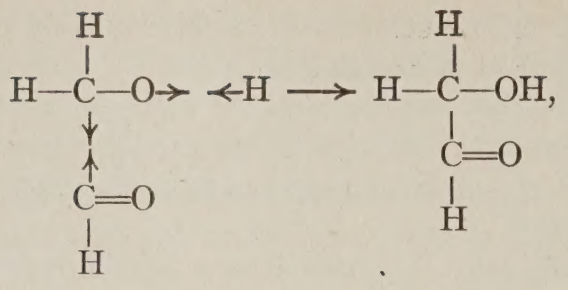
The products of this reaction are seen to be formic acid and hydrogen peroxide.

The third step may be a still further reduction of formic acid to formaldehyde, with the production of more hydrogen peroxide.

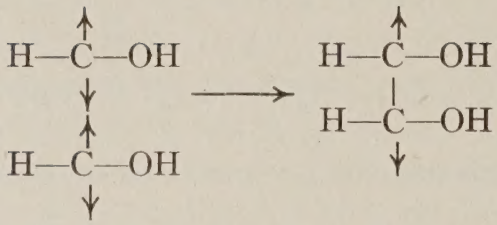
$$(3)\quad H{-}\overset{\overset{O}{\|}}{C}{-}OH + H_2O \longrightarrow H{-}\underset{\underset{H}{|}}{C} = O + H_2O_2$$

The hydrogen peroxide would be toxic, but nearly all living cells contain an enzyme, catalase, which breaks up H_2O_2 into $H_2O + O_2$, which are not toxic. The reduction seems to consist of taking the oxygen out of the two —OH groups of the original carbonic acid, leaving formaldehyde.

The final step, conversion of formaldehyde to sugar, requires reactive formaldehyde, and it can become reactive in several ways. Either the double bond of the oxygen may open, $H{-}\overset{\uparrow}{\underset{\underset{H}{|}}{C}}{-}O\longrightarrow$, or a hydrogen may break off, $H\rightarrow\ \leftarrow\underset{\underset{H}{|}}{C} = O$, or it may be formed in such a way as to possess reactive carbon, $H{-}\overset{\uparrow}{\underset{\downarrow}{C}}{-}OH$. Presumably all these forms of reactive aldehyde may exist in a solution of aldehydes; and to build up more complex aldehydes, all that is necessary is to bring the two kinds of reactive molecules together, thus:

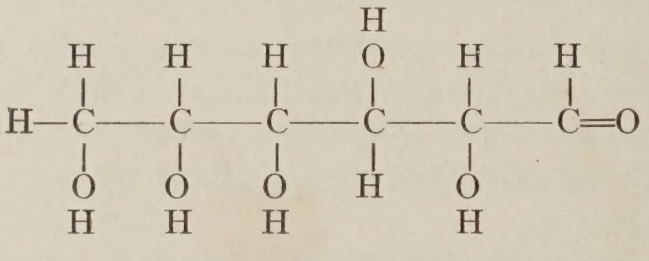


or



The first of these reactions would produce the two carbon, or biose, sugar glycol aldehyde. By successively adding molecules of formaldehyde in the same way, we would obtain a triose, tetrose, pentose, and hexose. In the plant the process runs mainly to the six carbon sugar, dextrose.

The resulting sugar, *d*-glucose, has the structural formula



Glucose and starch. — Glucose probably represents the first stable carbohydrate formed in most plants; yet there is some variation in this respect in different plants, and there is evidence that in some cases cane sugar, saccharose, is the chief product. This, however, cannot be looked upon as the first sugar of photosynthesis, as Brown and Morris, Parkin, and Davis and his coworkers supposed. It is quite possible, moreover, to divert some of the product into amides by a simple substitution of the amide radical, NH_2, for some H or OH radical. Thus, if the fifth group in the glucose chain became $HC(NH_2)$, the product would be glucosamin, a substance of quite different properties (see pp. 115–116). Like diversion by substitution might readily occur if only two or three formaldehyde molecules had come together. Such processes seem to be the initial steps in proteinsynthesis (p. 148).

The common main product, glucose, usually accumulates in the cells because it is formed faster than it can move away. Finally starch or some other stable product appears. The intervening steps are hypothetical. It seems that at a certain concentration glucose molecules show a tendency to combine with each other to form a compound sugar, maltose ($C_{12}H_{22}O_{11}$), which promptly compounds itself in like manner into a dextrin and finally into starch. This process always involves loss of water, and is known as condensation. The combinations occur rapidly, and the intermediate products are hence obscure. Perhaps the process takes place under the influence of third bodies, called enzymes; maltase and diastase in the cases here cited being the possible agents (but see enzymes, p. 173). The starch accumulates in minute granules within the chloroplasts (fig. 34), so their stroma may be the direct agent in organizing the starch, or at least may be the seat for the formation of the enzymes which bring this about. These grains have a definite structure and a rather uncertain composition (see starch, p. 113), for both of which the chloroplast itself may be responsible (see leucoplasts, p. 161). Reichert[1] has shown that each species of plant has specific starch grains, probably because of the specificity of the protoplasm which builds the grains.

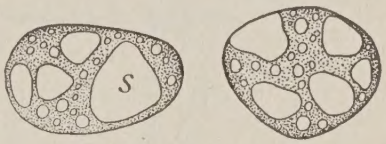


FIG. 34. — Two chloroplasts of *Rhipsalis*, with grains of starch (*s*) and minute oil droplets. — After SCHIMPER.

Removal of products. — If a leaf is isolated, the accumulation of the synthetic products may reach a point where it interferes with further photosynthesis; but in nature this does not occur. Use on the spot, or diffusion of such products as remain simple and soluble, or the digestion of the more complex and the insoluble ones by enzymes (p. 173) and subsequent diffusion, is constantly removing the new materials from the leaves and stems to other places where they may accumulate or be used (see translocation, p. 164). In darkness or weak light, the transportation facilities, temporarily overtaxed in full light, overtake the manufacturing; the laboratories are cleared, consumers are supplied, and the warehouses and distributing centers are filled with the surplus awaiting future use.

The by-product. — The by-product, oxygen, is used to some extent in respiration (p. 180); the excess diffuses to the surface, whence it

[1] Reichert, Edward Tyson. The differentiation and specificity of starches in relation to genera, species, etc. 2 vols. *Carnegie Inst. Pub.* No. 173. Washington. 1913.

escapes into the aërating system and thence into the air. The final step in its exit can be observed in water plants readily, because the constant accumulation in the air chambers leads to its escape as bubbles when the passages are opened by a cut or break (fig. 35). If the canals are intact, O_2 may become abundant enough in bright light to form bubbles on the surface, which rise as they become larger. The rising gases can be conducted by an inverted funnel into a test tube and analyzed; they are about 85 per cent oxygen, the remainder being other gases produced in other processes or coming out of solution from the water in and around the plant. So uniform is the evolution of O_2 by water plants that with precautions the number of bubbles given off in unit time can be used to exhibit the general effect of the three external factors, intensity of light, temperature, and supply of CO_2, on photosynthesis. It is not satisfactory for quantitative determinations unless greatly refined methods are used.[1]

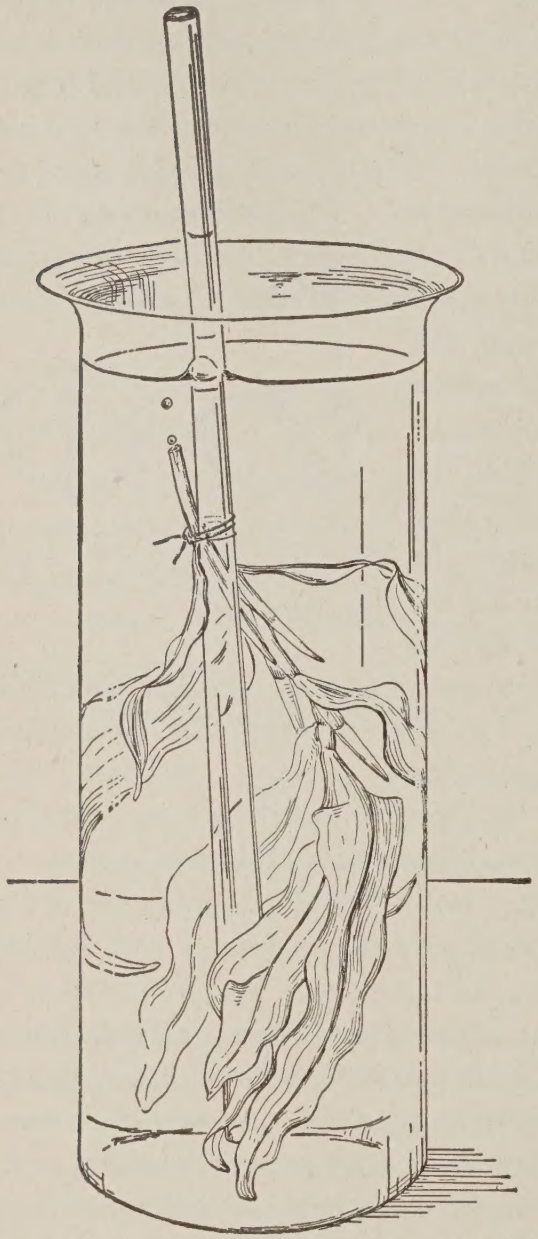


FIG. 35. — Upper part of a plant of *Potamogeton* attached to a glass rod and submersed, showing escape of gas bubbles (mostly oxygen) from cut end of stem in sunlight.

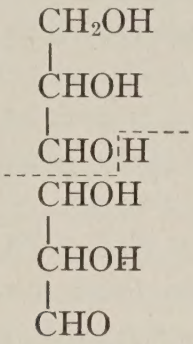
4. SYNTHESIS OF FATS

The fats probably are derived directly from the carbohydrates. The two constituents of the fats are, on the one hand, glycerol, and

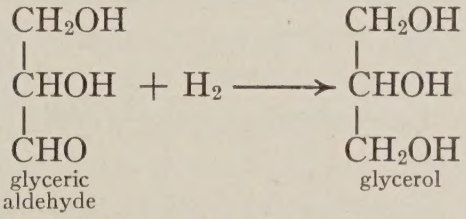
[1] Wilmott, A. J. Experimental researches on vegetable assimilation and respiration, XIV. Assimilation by submerged plants in dilute solutions of bicarbonates and acids: an improved bubble-counting technique. *Proc. Roy. Soc.* Lond. B. **92**: 304–327. 1921.

on the other, fatty acids, such as myristic, palmitic, stearic, and oleic acids.

Here again the exact steps of synthesis are not known, but we can picture reactions in such a way as to give a general idea of possible steps in the process. The sugar molecule can be broken in the middle to form two exactly equal molecules, thus:



The resulting substance is glyceric aldehyde, the triose or three-carbon sugar. Glyceric aldehyde may be reduced by use of hydrogen,



and we obtain in a very simple manner, glycerol, one of the constituents of the fats.

It is more difficult to understand how fatty acids may arise, but aldehydes like glyceric aldehyde or acetaldehyde, are probable starting points, or better still, pyruvic acid, $CH_3 \cdot CO \cdot COOH$, which may arise directly from the decomposition of sugars. This acid may break down to form acetaldehyde under the influence of an enzyme, carboxylase, which splits CO_2 out of the $-\overset{\overset{O}{\|}}{C}-OH$ group of acids. Then by a combination of the resulting acetaldehyde with pyruvic acid, longer chains of carbons may be built up, such a compound as $CH_3 \cdot CH : CH \cdot CH : CH \cdot CHO$ being formed by utilization of three molecules of the pyruvic acid. If we now reduce the chain with hydrogen where the double bonds occur, and oxidize the —CHO group to

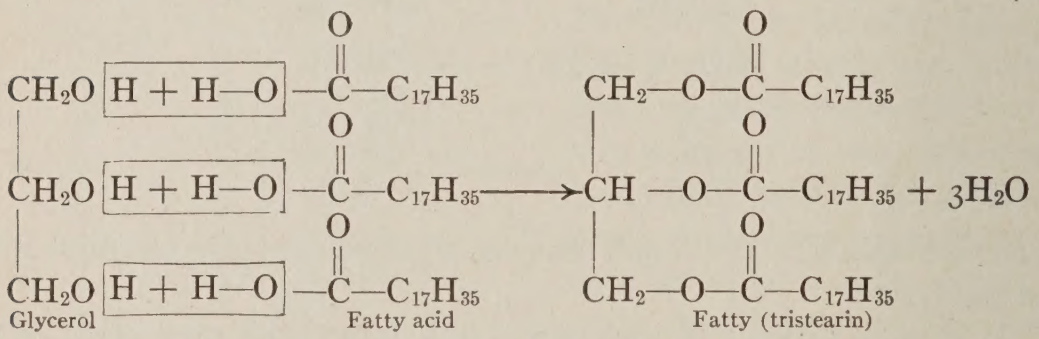
—COOH, we will have a fatty acid, caproic acid, found in the fat of goat butter. The reaction may be written as follows:

$$2\,CH_3 \cdot CH{:}CH \cdot CH{:}CH \cdot CHO + 4\,H_2 + O_2 \longrightarrow 2\,CH_3 \cdot CH_2 \cdot CH_2 \cdot CH_2 \cdot CH_2 \cdot COOH$$

(Unsaturated aldehyde) (Caproic acid)

As the acetaldehyde, coming from the pyruvic acid originally, has but two carbons, it is seen that every time we take another molecule of pyruvic acid into the chain, it adds but two carbons. Three molecules of pyruvic acid build a six-carbon acid, four molecules an eight-carbon acid, eight molecules a sixteen-carbon acid, and so on. Most plant fats contain 14, 16, or 18 carbons in the chain. Thus myristic acid is $C_{13}H_{27}COOH$, palmitic acid is $C_{15}G_{31}COOH$, and stearic acid $C_{17}H_{35}$ COOH. In order to produce these long chains we would have to start with 7, 8, or 9 molecules of pyruvic acid to produce one molecule of fatty acid.

Once we have both glycerol and fatty acids present, their union to form true fats is brought about by an enzyme, lipase, which can condense the glycerol and fatty acids to fat with the loss of water.



This fat is called tristearin because it contains three stearic acid molecules combined with one molecule of glycerol.

Many plants, such as cotton, olive, castor bean, flax, and peanut, store most of their food as oil. Corn also stores some oil in its seeds. Fats are the most highly condensed form of food made by plants. They are usually stored as droplets of fat in the cells of the storage organs where the fats are deposited.

5. THE SYNTHESIS OF PROTEINS

Proteins the end-product. — The formation of carbohydrates and fats are by no means the only processes of food making. Indeed

carbohydrate synthesis may be looked upon as merely the first stage in the construction of fats and proteins, of which carbohydrates are important components. As the living protoplasm appears to be composed chiefly of proteins (probably more complex and labile than in the non-living state), it is evident that protein foods are of the highest importance — indeed indispensable — for nutrition, since it is the protoplasm which grows, wastes, and needs repair. Proteins are, as it were, the highest type of foods; they represent the final stage of food making.

Inasmuch as the carbohydrates contain only carbon, hydrogen, and oxygen, while proteins contain in addition nitrogen and sulphur and in many cases phosphorus also, it is plain that they cannot be formed from carbohydrates alone. A strict carbohydrate diet is as unsuitable for plants as it is for animals. Some materials must be supplied from which nitrogen, sulphur, and phosphorus can be obtained.

Source of nitrogen. — As the air contains 78 per cent of nitrogen, the atmosphere would appear to be a natural source of this element. But though the nitrogen is everywhere dissolved in the water of the plant, and can enter and leave it freely, no plants are known to be able to use it in this uncombined form, except certain bacteria, which have been discussed in connection with the nitrogen of the soil. Almost all plants, therefore, must get combined nitrogen. This is found in soils as nitrates of various bases, *e.g.* calcium, magnesium, potassium, and sodium; and when a soil is deficient in nitrogen, such compounds are important constituents of the fertilizers, natural and artificial, which are added to it. The nitrates in the soil result mainly from the decay of organic matter in it. The later steps in the process are controlled by certain bacteria in the soil which bring about the oxidation of ammonia to nitrites, whereupon others oxidize the nitrites to nitrates. The very fertility of arable soils, therefore, depends on the microscopic organisms living in them, which prepare the way for the larger plants.

The biological relations in a fertile soil are very complex and are not fully understood. There are very many kinds of bacteria and fungi present in the decaying humus, and the number of individual organisms in a given soil mass is beyond our power to imagine. Even in barren soils there may be as many as 100,000 bacteria per gram, or forty-five million in a pound of the soil. In a rich garden loam the bacterial population may exceed 1,500,000 per gram, or

something like six hundred and seventy-five million in each pound Contaminated soils are still far richer in bacterial life. In a back yard where slops had been freely thrown upon the surface of the ground, the soil was found to contain 11,500,000 bacteria per gram, equal to more than five billion organisms to each pound of soil. These organisms feed upon the humus and cause the various stages of decay which render the humus elements available again for the use of living plants.

In addition to bacteria there are a good many kinds of protozoa, unicellular animals, which inhabit soils. Among these, there is a kind of Amoeba which is called *Dimastigamoeba.*[1] This creeping amoeba is predatory upon the bacteria, devouring great numbers of them as it creeps around in the soil interspaces. If the amoeba devours too many of the bacteria, especially of the favorable kinds, the soil may be less fertile because of the destruction of the bacteria.

It has been found that partial sterilization of the soil, as by heat or anaesthetics, increases its fertility later on.[2] There is usually a very large increase in the bacterial count of the soil following the partial sterilization. The explanation offered is that the partial sterilization may more effectively kill the amoebas than the bacteria; and when the amoebas are nearly all destroyed, the bacteria multiply without encountering the usual number of predatory protozoa.

Russell and his co-workers at Rothamsted have noted periodic increase and decrease in the number of bacteria in the soil,[3] and they find these fluctuations in bacterial number associated with changes in the number of amoebas. As the latter increase, the bacteria decrease; but soon the amoebas seem to die off, possibly due to their bacterial food becoming too scarce, and then the bacteria once more have opportunity to increase in numbers.

These complex relationships must play a part in the fertility of the soil, but we cannot at present picture the exact relations between the biological conditions of the soil, and fertility. These relations still require much study on the part of agronomists and plant physiologists.

[1] Russell, E. J. *Plant Nutrition and Crop Production.* pp. 71–76. Univ. Calif. Press. 1926.

[2] Russell, E. J., and Hutchinson, H. B. The effect of partial sterilization of soil on the production of plant food. *Jour. Agr. Sci.* **3**: 111–144, 1909; and **5**: 152–221, 1913.

[3] Russell, E. J. *The Microörganisms of the Soil.* chap. v. Longmans, Green & Co. 1923.

Some of the fungi of the soil prevent otherwise fertile soils from producing good crops. The cabbage yellows organism (*Fusarium conglutinans*), flax wilt (*Fusarium lini*), tobacco root rot (*Thielavia basicola*), corn root rots, cotton wilt, and many others are important in connection with the problems of soil sanitation. There is hope that crops may be improved by selection for resistance to infection by soil organisms. We already have wilt-resistant cotton, yellows-resistant cabbage, and root-rot-resistant tobaccos. Future breeding experiments are expected to provide resistant strains of plants to overcome many of the soil-borne diseases of plants.

Source of S and P. — The sulphur and phosphorus needed are obtained by the green plants from sulphates and phosphates which dissolve in the soil water. The decaying vegetable matter also returns sulphur and phosphorus to the soil. The mercaptans and other sulphur-containing compounds are converted into H_2S, and this is oxidized to sulphate, by various sulphur-using bacteria, as was shown in the discussion of chemosynthesis. Few soils lack these elements, though for cropping the phosphates may be insufficient or may be so reduced as to interfere with full development. "Land plaster" (gypsum, or calcium sulphate) is sometimes applied to fields; but it probably has more beneficial effects on other qualities than on the composition of the soil. Phosphates are an important part of artificial manures.[1] The best phosphatic fertilizer is acid phosphate, but bone meal may be used when it is known that phosphorus only is needed. No fertilizer element should be used unless it is known to be a limiting factor in crop production. In the case of both nitrogen and phosphorus it is highly important, if immediate effects are desired, that the compounds be such as are "available," and compounds can be available only when they are soluble or readily become so.

Raw materials. — The nitrates, sulphates, and phosphates enter the larger plants through the roots. These are the mineral salts which are most necessary for the well-being of the plant, because they are needed for protein synthesis. Like CO_2 and H_2O, they have been called "foods"; but it is far better to look upon them as raw materials out of which, with others, food can be made.

[1] The whole subject of the relation of manures and fertilizers to the soil and crop is in a very unsatisfactory state and needs further investigation before the practice and results can be explained.

Given carbohydrates (finished and partly torn up again, or " in the making ") plus nitrates, sulphates, and phosphates, most plants can make proteins. There is no set of plants to which proteinsynthesis is restricted, as is photosynthesis to the green plants. Yet there are plants (certain bacteria, for example) which require their nitrogen supplied in other forms than nitrate, and some even which can use nothing less complex than proteins. Here we may properly speak of assimilation rather than of synthesis.

No special organs. — In the larger plants proteinsynthesis is not restricted to a particular organ. Neither chlorophyll nor light is essential to it, for it is carried on freely by fungi which have no chlorophyll, and it is doubtful, in spite of much experimenting, whether light has any influence upon its rate, excepting that light provides for more rapid synthesis of the carbohydrates which are necessary for the building of the amino-acids. Since carbohydrates are usually the basis of proteinsynthesis, the leaves, in green plants, are the chief seat of this process; for in the leaves carbohydrates are being made, and to them stream the dilute watery solutions of salts, brought *via* the xylem bundles by evaporation.

Process. — So long as the constitution of proteins remains unknown it will be impossible to describe the process by which they are made. Inasmuch as all proteins on decomposition yield amino-acids, and the simpler proteins are certainly formed from these acids by condensation, it is supposed that carbohydrates are converted into amino-acids first, by the introduction of NH_2-groups here and there, and that these amino-acids link themselves together, some becoming modified by the incorporation of sulphur and phosphorus atoms, and so form proteins of various kinds.

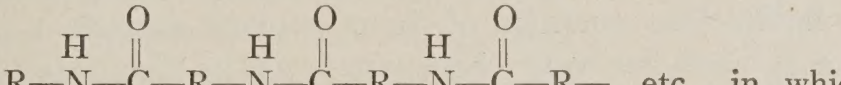
As in the case of carbohydrates and fats, the steps of proteinsynthesis are not accurately known. The nitrates absorbed by green plants from the soil are reduced in the plant, probably by some reductase enzyme. By this reduction ammonia arises, from which the NH_2-group is obtained. By incorporating the NH_2-group into the reactive aldehydes, and oxidizing the aldehydes to acids, we would obtain nitrogen-containing acids, which are called amino-acids. Acetaldehyde, with an NH_2-group substituted for one of the hydro-

$$\begin{array}{l} CH_3 \\ | \\ CHO \end{array} + NH_3 + O_2 \longrightarrow \begin{array}{l} CH_2NH_2 \\ | \\ COOH \\ \text{(glycine)} \end{array} + H_2O$$

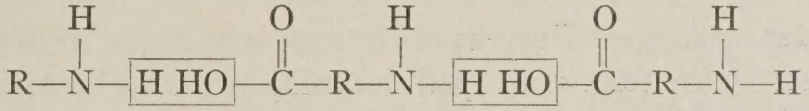
gens, and with oxidation to acid, would yield glycine, one of the simplest amino-acids. There are more than twenty kinds of amino-acids known, and these are readily joined together by protein condensing enzymes.

Eckerson[1] has brought forward evidence that the nitrate reduction occurs in some plants in the phloem regions of the stems, where the reaction is slightly alkaline, say pH 7.2.–7.6. The presence of some aldehyde, like acetaldehyde or some sugar, seems to be necessary. When nitrate is given to a nitrogen starved plant, one can soon find the nitrate distributed through the plant, after which ammonia is produced. This is later converted into amino-acids, and these finally into proteins. The sulphur is used mainly in building cystein, cystine, glutathione, mercaptans and mustard oil glucosides when these are present, as in the Cruciferae. Phosphorus is used mainly in building the nucleoproteins, for the nucleic acids found in these proteins contain phosphoric acid.

Our ideas of the structure of the protein molecule are undergoing a change at the present time. Following Fischer's work on the proteins, we have imagined that the amino-acids were linked together in long chains, of several hundred amino-acids. The linkage, called the peptide linkage, may be represented thus:



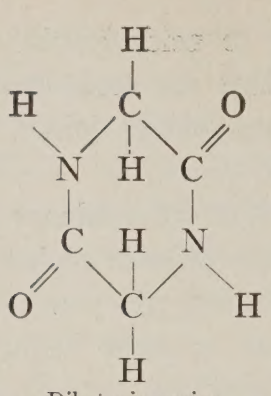
, etc., in which R represents the main body of an amino-acid, with its NH_2-group combined with the carboxyl group, —COOH, of the neighboring amino-acid. In this condensation a molecule of water is formed at each linkage.



Recent work by Abderhalden[2] and others indicates that the amino-acids may be tied together partially at least in rings, and not necessarily in long chains. These rings are heterocyclic, that is, they contain both carbon and nitrogen atoms, as in the compound known as diketopiperazine.

[1] Eckerson, S. H. Protein synthesis by plants. I. Nitrate reduction. *Bot. Gaz.* **77**:377–390. 1924.

[2] Abderhalden, E., and Komm, Ernst. The anhydride structure of proteins. *Zeitschr. Physiol. Chem.* **139**: 181–204. 1924.



Diketopiperazine

Abderhalden thinks that the proteins may be made up in part of substituted diketopiperazide rings held together in the protein molecule by secondary valencies. In some cases as high as thirty to forty per cent of the proteins have been found to consist of such rings. This idea has not yet had satisfactory confirmation.

It is perhaps best merely to remember that the proteins are very complex, with very high molecular weights, and that they yield on hydrolysis mainly amino-acids, which may be present either in chains or rings in the protein molecules. The synthesis of these molecules involves the presence of enzymes which condense amino-acids into chains or rings with loss of water. The main enzymes which do this work are peptase and ereptase which have power to synthesize proteins whenever the condition of the protoplasm permits it. In the presence of much free water these same enzymes digest the proteins, but reverse their action when dehydration reverses the equilibrium of the reaction in which they take part.

6. OTHER WAYS OF GETTING FOOD

Dependent plants. — The green plants are sometimes distinguished from others by the term *autotrophic*, meaning that they nourish themselves by their ability to make in their own bodies the most important foods, the carbohydrates. All others are *heterotrophic* plants, signifying that they secure food in a different way. The more important ways of securing food without having to manufacture it are now to be described.

Among the many thousand species of heterotrophic plants, the bacteria and fungi hold the dominant place. A few seed plants lack chlorophyll entirely, such as the Indian pipe (*Monotropa*), beech drops (*Epifagus virginiana*), dodder (*Cuscuta*), etc.; and some have only

partially lost it, or with a good supply nevertheless have the nutritive habits of the non-green plants.

The families in which such dependent species are prominent are the Loranthaceae, Rafflesiaceae, Scrophulariaceae, Orobanchaceae, and Balanophoraceae.

If a plant cannot make carbohydrates, it must of necessity get food directly or indirectly from some plant that can. The direct way of doing this is to live on or in a live green plant. The indirect way differs only in that the food secured is more remote from the original food maker. Thus, a plant may live upon or in some animal or some non-green plant, or upon the dead bodies of these, more or less decayed and disintegrated. Indeed, decay and disintegration are only the obvious evidence that plants (chiefly the minute bacteria and fungi) are living upon such a dead body. And not infrequently death itself is simply the result of the vigorous development of such creatures on or in the body of a once healthy organism.

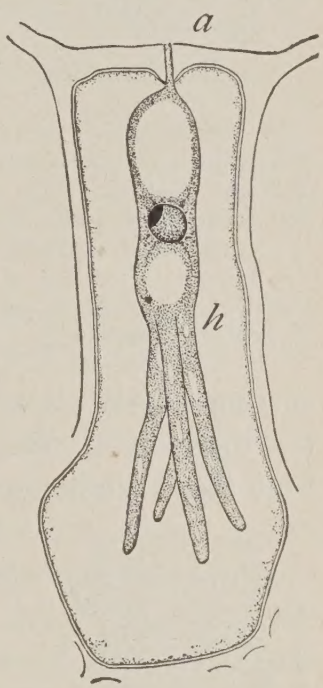


FIG. 36. — An epidermal cell of a grass (*Poa*) penetrated by a branched haustorium (*h*) of a fungus (*Erysiphe graminis*); the mycelial hypha to which the slender penetrating tube (*a*) is attached is not shown. — After SMITH.

Parasitism. — An association between two live organisms is known as *symbiosis*. When one symbiont obtains its food from the other, the relation is called parasitism, and the two are known respectively as *parasite* and *host*. As a rule the food maker is called the host, and the other the parasite; if neither or both be food makers, the larger is distinguished as the host. Thus, fungi are parasitic on leaves or twigs or in the wood of trees, or on animals; "beechdrops" (*Epifagus virginiana*, a small flowering plant) is parasitic on the roots of the beech tree; mistletoe is parasitic on elms, etc. This relation requires the closest contact between the cells of parasite and host, and the parasite even penetrates the cells of the host in many cases. The smaller parasites, such as fungi, may grow bodily through cells, doubtless dissolving the wall by some enzyme or by forming an appressorium and forcing its way into the cell by mechanical pressure; or it may send into them short branches, called haustoria (fig. 36), through which the food enters the

parasite. A vascular parasite, the dodder, which twines extensively over coarse herbs, sends into its host short branches, likewise called haustoria (fig. 37), whose vascular strands come into the most intimate contact with those of the host. (See *Ecology* on parasitism.)

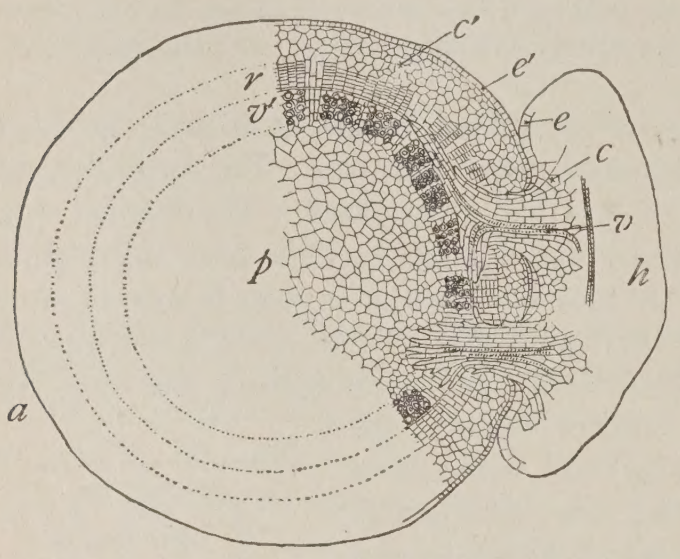


FIG. 37. — Section of stem penetrated by haustorium (*h*) of dodder (*Cuscuta*). The vascular tract (*v*) of the parasite with its hadrome comes into contact with the same region (*v'*) of the host; *p*, central pith of the host; *c*, cortex of the parasite; *c'*, cortex of the host; *e*, epidermis of the parasite; *e'*, epidermis of the host; *r*, cambium of the host, highly magnified.

Partial parasites. — When such complete contact has been established, it is difficult to determine what or how much material migrates from host to parasite. Colorless parasites, of course, must get all their food from the host. Certain green parasites undoubtedly could live by getting merely water and its dissolved salts, for they can make food for themselves. Hence they are known as partial parasites. But that they completely restrict themselves to such food materials and do not admit any real food is quite improbable, in view of the intimate union between the two.

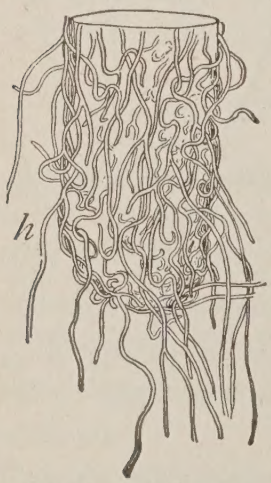


FIG. 38. — Ectotrophic mycorhiza of European beech (*Fagus sylvatica*); *h*, hyphae. — After FRANK.

Mutualism. — The support of the parasite by the host may result in no considerable injury or even weakening. Indeed, many cases have been described in which the association suggested a partnership, whence the term *mutualism*. From another point of view the relation resembles that of master and slave, whence the term *helotism*. (See *Ecology*.) The lichens (*Morphology*, p. 78) furnish the classical example. Yet even here the algae are somewhat restricted in development by the constant drain upon them, though perhaps they can work at food making longer because the encompassing fungus by its spongy

texture retains rainwater longer than would the algae alone. Mycorhiza[1] is another instance of so-called mutualism, in which fungi associate themselves with the roots of certain plants, especially the oaks (Cupuliferae), the heaths (Ericaceae), and the orchids (Orchidaceae). Sometimes they jacket the rootlets with a weft of filaments (ectotrophic mycorhiza, fig. 38), and sometimes they penetrate the cortical cells, forming a tangle about the nucleus (endotrophic mycorhiza, fig. 39). The fungi are supposed to aid the root in acquiring water and food materials (especially nitrogen compounds, which they themselves may form from the free nitrogen of the air) from the soil. Certainly they derive some food from the root, and injury to the root is suggested by its stubby form and the frequent absence of root hairs. In fact, the more the cases of so-called mutualism are studied, the more it becomes evident that they are only cases of modified parasitism, with minor injury to the host. (See *Ecology*, on reciprocal parasitism.)

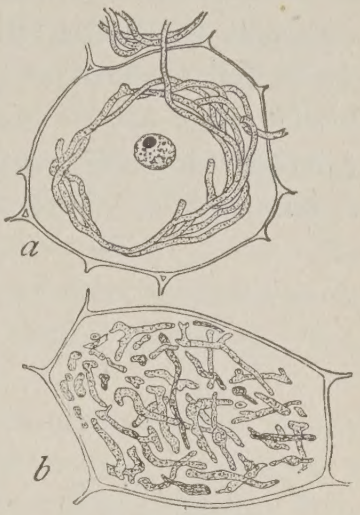


FIG. 39. — Endotrophic mycorhiza of *Neottia*: *a*, host cell with active fungus hyphae; *b*, cell with degenerating hyphae. — After MAGNUS.

Injury by parasites. — On the other hand, the drain on the food resources of the host may be severe, so weakening it that it succumbs to adverse conditions which otherwise could be overcome. Quite apart from this weakening for lack of food, the parasite may act as a stimulus to local growth, or it may produce injurious substances which cause local or even general death. The location of a parasite is often marked by deformities; leaves are crinkled or thickened, as in peach curl; circumscribed swellings of peculiar and fantastic or beautiful forms (galls) grow on leaves or stems (fig. 40); even large tumors are formed, as in the black knot of cherry and plum trees. Local death is another common mark of the presence of a parasite. The fire blight of apple and pear trees, due to parasite bacteria, gets its name because young shoots are killed for a distance of 20 to 50 cm., and the withered brown leaves make the tree look as though it had

[1] Rayner, M. C. Mycorhiza. *New Phytologist* **30** : 1, 65, 171, 248, 338–372. 1926. (See also continuation of series in *New Phytologist* **31** : 1927. These papers constitute a review of the subject to the present time.)

been scorched by a fire. General death in large plants is seldom produced by a parasite unless it interferes with the water supply or invades the entire organism. In wilt disease the parasite blocks the tracheae, interfering with the supply of water to the leaves, and death follows with surprising suddenness. In other cases, since in plants there are no means for quick distribution of poisons locally produced, nor any regulatory centers whose injury upsets the whole system, death is likely to be merely local. In animals, on the con-

FIG. 40. — Galls: *a*, on leaf of rose; *b*, on stem of grape.

trary, a parasitic plant, restricted to a limited region, may produce poisons which are quickly spread through the body by the blood, attack the central nervous system or important viscera, and soon cause death. Thus, in diphtheria, the bacteria flourish chiefly in the throat, where they may produce no serious lesion, but the toxins produced reach the heart and kidneys and sometimes fatally injure them.

Some parasitic organisms have become very important economically because of the losses they cause to agriculture, forestry, and other industries. The black stem rust of wheat, *Puccinia graminis tritici*, causes millions of dollars of loss in the grain-growing regions every year. An attempt is being made to reduce this loss by eradication of the common barberry.[1] While this may decrease the ravages some,

[1] Thompson, N. F., and Dickson, J. G. Fighting black stem rust of grains by eradicating the barberry. *Wisconsin Agr. Exp. Sta.* Bull. 357. 1923.

it is well known that uredospores winter over in the southern states, and they probably winter over on wild grasses in Canada. It is not likely, therefore, that barberry eradication will ever eliminate rust from our wheat fields. But it may reduce the attacks to the point where they are not calamitous to the regions where the attacks have been most severe.

The chestnut blight, *Endothia parasitica*, has caused enormous losses of timber in the Appalachian chestnut region.[1] A great deal of money was spent in efforts to control this fungus without avail. The chestnut tree has been virtually eliminated as a timber tree in eastern North America. The parasite kills the bark until it girdles the tree, after which the tree dies.

The white pine blister rust is another serious disease whose steady spread in spite of the strenuous efforts made to control it has been a prominent feature of the recent battles with plant disease.[2] The organism, *Cronartium ribicola*, lives on species of gooseberries and currants for its intermediate stage. It is doubtful that the destruction of gooseberries and currants would eliminate the parasite by breaking the life cycle. Such an attempt would be very expensive, and of doubtful value; but one feels that almost anything is justified in the face of such menacing diseases as those mentioned.

Saprophytes. — The association of a plant with a dead organism or organic débris is called *saprophytism*, and the live member is a saprophyte. Since a parasite may kill its host and then continue to live upon the body, the distinction between parasites and saprophytes is not always clear. Thus there are obligate parasites and obligate saprophytes; plants, namely, that are obliged to live in one relation or the other. Correspondingly there are facultative parasites and facultative saprophytes, which may pass part of their lives in one way and part in the other or wholly in either. Often the full cycle can be completed only if the given plant can establish the preferred relation.

The main saprophytic organisms are the decay bacteria, various kinds of molds, and our commoner mushrooms. Bread mold is a typical saprophytic fungus, with mycelium in the substrate, and sporangiophores rising into the air for the scattering of spores.

[1] Gravatt, G. F. The spread of the chestnut blight in the southern Appalachians. *Jour. Amer. Leather Chem. Assoc.* **19**: 138–146. 1924.

Heald, F. D. *Manual of Plant Diseases*. pp. 596–610. 1926.

[2] Spaulding, P. Investigations of the white pine blister rust. *U. S. Dept. Agr. Bull.* 957: 1–100. 1922.

Saprophytes are very numerous and varied. They may be superficial, or may penetrate the substratum thoroughly, showing finally at the surface only the reproductive bodies. The very fact that they are getting food from the dead organism indicates that they are consuming it. Inasmuch as they often must digest the food before it can enter their bodies, they disintegrate the body on which they feed. In the course of this digestion and disintegration, many and varied chemical reactions occur, some incited by the saprophyte, some incidental to the changes it produces. These are summed up for fluid media under the term *fermentation*, and for solids under the terms *decay* or *putrefaction*. Certainly in fermentation (p. 184), and probably also in putrefaction and decay, some of the most striking reactions are not connected with food getting, though apparently they are entirely similar thereto.

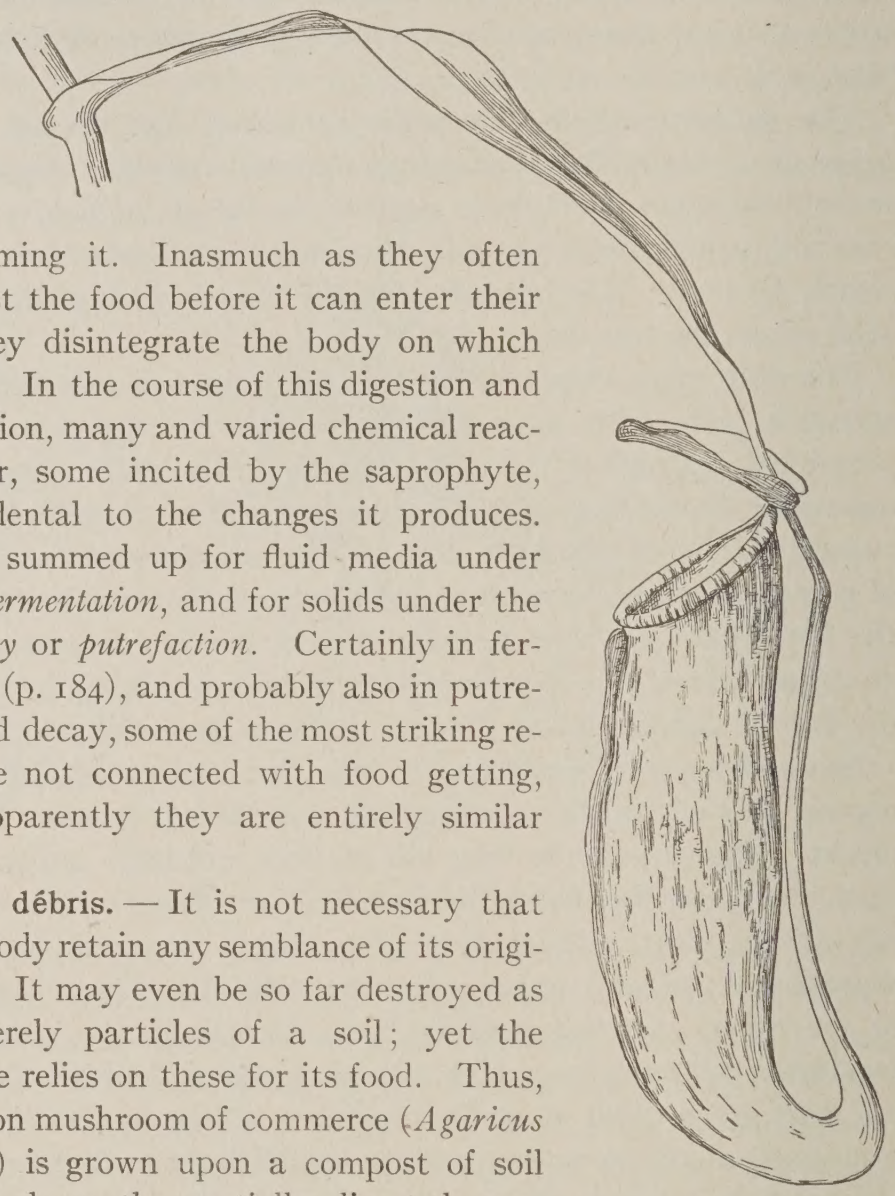


FIG. 41. — Leaf of *Nepenthes Mastersiana*. — From a photograph by G. W. OLIVER.

Organic débris. — It is not necessary that the dead body retain any semblance of its original form. It may even be so far destroyed as to be merely particles of a soil; yet the saprophyte relies on these for its food. Thus, the common mushroom of commerce (*Agaricus campestris*) is grown upon a compost of soil and horse dung, the partially digested remnants of grain and hay furnishing the food for the mycelium. Indeed, as has already been shown, every soil containing organic matter supports a varied if minute flora, whose operations are often indispensable to the welfare of larger plants.

Succession. — Nothing is more striking than the succession of saprophytes that live upon a dead organism and finally dispose of all its

organic matter, each appropriating a suitable part and reducing that to the most simple and stable compounds, until finally it "returns to the dust whence it came." This emphasizes, too, the striking differences between saprophytes in their use of offered foods — differences which at present are quite inexplicable. A classification of saprophytes according to the sort of food on which they thrive best has been made; but this expresses only in a summary way our very imperfect knowledge of their nutrition.

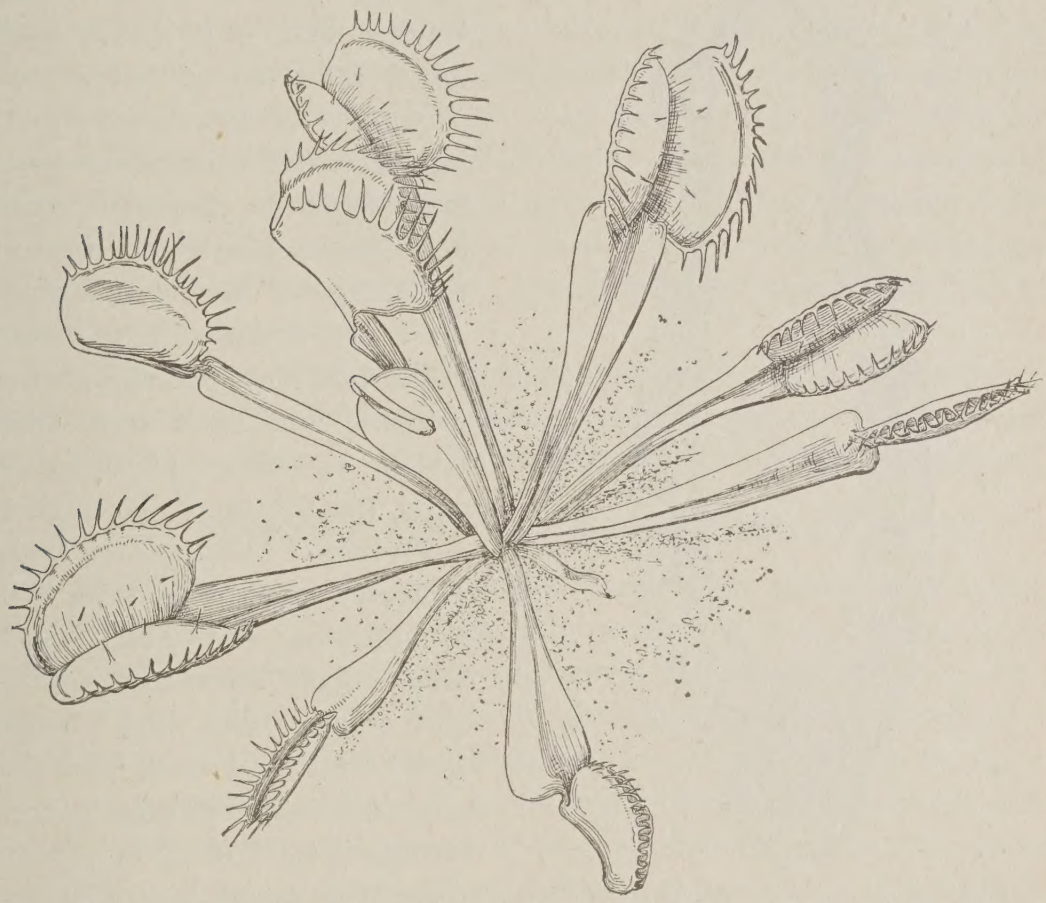
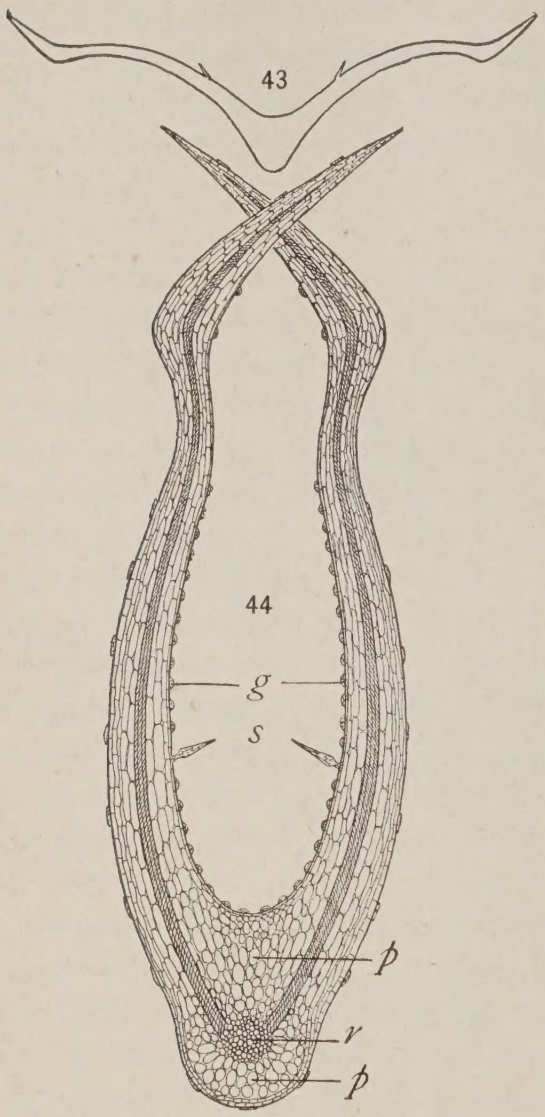


FIG. 42. — A rosette of leaves of Venus's flytrap (*Dionaea muscipula*) seen from above. — From a photograph by G. W. OLIVER.

Insectivorous plants. — Besides the ordinary parasites and saprophytes, there are a few rather isolated cases of green seed plants which have special apparatus for capturing small animals and digesting them. Some are submersed water plants, some grow on land. They are collectively known as insectivorous or carnivorous plants, but the methods of capture are quite diverse. Some of them possess pitchers or chambers of some kind in which the insects and other animals are

caught; some have power to produce active movements in the capture of their prey, and some merely have adhesives which glue the insects fast when they happen to alight, as in the Portuguese Drosophyllum.



FIGS. 43, 44. — Cross sections of the terminal lobes forming the "trap" of *Dionaea:* 43, enlarged view, closed position, diagrammatic; *g*, digestive glands; *p*, *p*, parenchymatous tissues whose varying turgor opens and closes the "trap"; *s*, sensitive bristles; 44, outline, on a smaller scale, of same in open position. — After KNY.

Pitcher plants. — The pitcher plants, *Sarracenia*, *Darlingtonia*, *Nepenthes* (fig. 41), and *Cephalotus*, have part or all of the leaf trumpet-like, pitcher-like, or cuplike, holding more or less water. The sides have stiff downward-pointing hairs, slippery areas of treacherous footing, deceptive translucent spots away from the concealed opening, one or all, which prevent the escape of insects that wander in and sooner or later drown in the fluid; whence nitrogenous compounds derived from their bodies by decay or digestion enter the tissues of the pitcher.

Flytrap. — Venus's flytrap, *Dionaea* (fig. 42), has leaves with two terminal lobes about 1 cm. long, hinged about the midrib, and fringed with long slender teeth, which interlock when the lobes shut together (figs. 43, 44). On the surface of each lobe are three large sensitive bristles, and if one of these be bent so as to compress the basal group of cells the lobes shut like the two jaws of a trap. Insects, flying or crawling, which come into contact with the bristles are often caught. Then the glands upon the upper (inner) surface pour out a digestive fluid, the proteins are reduced to such simplicity that they can enter the tissues, and after a few days the leaf opens again. Its water mate, *Aldrovanda*, has a

similar but smaller trap, by which minute swimming crustaceans, *Daphnia*, *Cyclops*, etc., are often caught.

Sundew. — *Drosera*, the sundew, has its leaves (fig. 73) fringed and covered above with stalked glands that secrete a viscid transparent fluid, in which small insects alighting may become enveloped by their own struggles, and further (in our species) on account of the inflection of the stalks of the glands. When an insect is caught, the character of the secretion changes; it becomes more watery and contains an enzyme which digests proteins. That the products enter the plant and are advantageous has been shown by comparing fed and unfed plants in the same pot. Those on whose leaves tiny bits of meat and egg were placed were larger and thriftier, and had more flowers, as well as more and larger seed, than the ones which grew under identical conditions without feeding. However, plants given enough nitrate through their roots do not need to receive animal food. On the other hand, plants fed nitrates do not lose their power to respond to stimulation by insects that frequent these plants.

The capture of insects probably supplements a scanty supply of nitrogen obtained from the soil nitrates; but too little is known of the ecology of such plants to establish this explanation as at all conclusive.

7. THE STORAGE AND TRANSLOCATION OF FOOD

Surplus food. — A part of the food made by a plant is promptly utilized in the making of new tissues (growth) and in the repair of the protoplasm which has undergone changes in the course of its activity. Another part of it is oxidized directly to furnish energy for growth and other work. Although most plants use foods immediately in these three ways, to produce new parts, to repair old parts, and to provide energy for work, yet most plants, at least at some period of their existence, make more food than they actually use at the time. The surplus is then stored for a longer or shorter time, until it is required. But it may never be used.

Storage places. — Accumulation of food may take place in the very part where it is made; but usually, if there is any room there, it is insufficient; and to judge from the infrequent storage in food-forming organs these two functions are not fully compatible. So when there is any considerable surplus of food, it migrates to some more or less specialized storage organ. In the lower plants these are relatively simple, for ordinarily such plants make little excess food. In *Marchantia*,

for instance, the colorless parenchyma of the lower part of the thallus is accounted the storage region. In the pteridophytes and spermatophytes, any one of the larger organs, root, stem, or leaf, may become the seat of food accumulation but the principal storage region of many kinds of plants, particularly the cereal grains, is the seed. In many of our horticultural varieties of plants, the ovary (seed pod) becomes fleshy, and the storage of foods in them produces our fruits. Very often there is marked change in structure and form of the storage tissue.

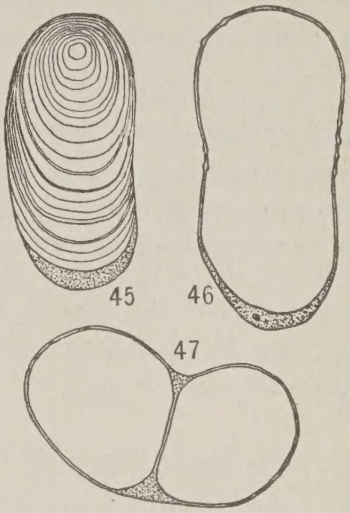
Parenchyma increased. — The characteristic change in structure of storage regions consists of an exaggerated development of parenchyma, in which chiefly the food accumulates. This may be the parenchyma of the cortex, or of the vascular bundles, or of the pith; or all may be involved. One noteworthy point is that the storage tissues are composed of live cells, even though, as in some ferns, they are very thick-walled. It is to be observed also that the reservoirs of food are usually located in parts that persist through a dry or cold season unfavorable to growth, and that have rudimentary growing points capable of quick and vigorous development by using the adjacent surplus foods. So the seeds, bulbs, tubers, rhizomes, etc., are organs of propagation, and by way of attaining that end become also organs of storage. (See *Ecology* on seeds, bulbs, and tubers.)

Storage cells active. — The storage of food is not merely a stuffing of passive cells with surplus food; it involves the activity of the storage cells themselves, at least for the accumulation of the food, and usually also for the mobilization when this food is about to travel to growing regions where it is subsequently used. The process of mobilization is commonly called digestion (see p. 170), and seems to be the reverse of the process by which the storage forms of food are produced.

Storage forms. — The storage forms of food are chiefly starches, sugars, hemi-celluloses, inulin, fats, and proteins. From this list it will be apparent that carbohydrates predominate, and quantitatively they form much the greater part of stored food.

Starches. — Starches are stored in the form of grains, many having a form characteristic of the plant in which they are found. The grains are organized by the activity of cell organs called leucoplasts or amyloplasts (figs. 45–47), which seem to take the material as it comes to the cells, perhaps as glucose, and combine it into larger and more complex molecules, that finally become starch. This is disposed in the

interior of the leucoplast as one or more grains, which at length stretch it enormously, or even rupture it. The actual structure of the grain is believed to be that of a spherite; that is, it is composed of a multitude of microscopically minute, threadlike crystals, radiating from its organic center. If more than one such crystal starts in the leucoplast, a compound or aggregate grain may result (fig. 47). The grains may show irregular layers (fig. 45), this appearance signifying differences in the proportion of water, composition of material, etc., doubtless determined by variations in the available sugars and other conditions during the growth of the grain.



FIGS. 45–47. — Starch grain and leucoplasts of *Pellionia*: 45, simple starch grain with leucoplast in position; 46, leucoplast alone of a similar grain; 47, leucoplast of a twin grain. × 900. — After MEYER.

It has been demonstrated by Reichert that each kind of plant possesses specific kinds of starch grains, especially with reference to the physical effects on polarized light.

The specificity of starch may be related to stereoisomerism, which may be traceable to the stereoisomerism of the protoplasm of the leucoplast which forms the starch grain.

The starchy reservoirs are sources of important foods for men and animals, as well as plants. Many of our farm and garden crops are such storage organs, greatly improved and enlarged by breeding. Potatoes, sweet potatoes, yams, all the cereals, peas and beans, arrowroot, sago, and tapioca are widely used plant products, whose most abundant constituent is starch. The extraction of starch for commercial purposes, especially from potatoes and corn, is an industry of considerable magnitude, as is also the production of alcohol by the fermentation of glucose derived from the starch of these plants. The following table shows the approximate starch content of some common food reservoirs, in percentages of their dry weight.

In seeds of rice	68	In seeds of navy beans .	45
In seeds of wheat . . .	68	In seeds of flax . . .	23
In seeds of corn . . .	60	In seeds of almond . .	8
In seeds of pea	52	In tuber of potato . . .	80

Sugars. — The chief storage form of the sugars is saccharose, or cane sugar. While glucose and fructose may be counted as constituents of almost every active cell, they do not accumulate in nature to any great extent, whereas saccharose in some plants, such as sugar cane, beet,

and maple, is almost the only form of surplus food, and in many it accompanies the reserves of starch. The commercial supply of sugar is obtained chiefly from cane and beet, while sorghum, maple, and certain palms furnish a relatively small or local supply.

Sugar is extracted from cane by crushing and washing, clarifying the liquor, and concentrating it. Beets are finely sliced and the sugar is extracted by diffusion, then recovered by clarification and concentration of the solution. The cultivated races of beet now average nearly 15 per cent of sugar, with some samples going over 20 per cent, as against less than 7 per cent when breeding began. Cane juice yields 10–18 per cent, and maple sap 2–5 per cent of saccharose. The refining of sugar by redissolving and purifying removes the coloring and flavoring matters which give to crude sugars from different plants their distinctive taste.

" Reserve cellulose." — This name has been applied to food accumulated upon the walls of cells; yet the substances are quite different from the cellulose which forms the permanent part of the wall, and should rather be called *hemi-celluloses*. They consist often of mannans and galactans, which on digestion yield mannose and galactose, sugars that are quickly transformed into other compounds. The hemicelluloses are especially common in the endosperm of seeds, and are used as food by the embryo in germination. They are deposited in layers on the interior of the cell walls, sometimes to the great reduction of the lumen; yet through the pits in the thickened walls the protoplast in each chamber maintains communication by slender threads with its neighbor. This excessive thickening imparts to such seeds a hornlike toughness, as in the coffee " bean," or even a bony hardness, as in the date " stones." Sometimes cotyledons and even bud scales have like deposits on their cell walls.

Inulin. — Inulin is comparatively restricted, being characteristic of a few large families, mainly the compositae (and occasional elsewhere). It occurs dissolved in the cell sap, especially of subterranean organs like roots of dandelion, and tubers of dahlia and artichoke. It is a very complex carbohydrate, though less so than starch, having a formula $n(C_6H_{10}O_5)$, where n is probably as much as 12 or 18. Whereas starch is built from glucose units, inulin is formed by the condensation of fructose units, and is comparable in complexity with some of the dextrins, which starch yields by digestion. When inulin-containing tissues are put into strong alcohol, the inulin is deposited as spherites.

Fats. — Fats are among the most important and valuable of surplus foods. In most plants they exist as small drops of oil in the protoplast; but in some cases, as in cacao, they are solid at ordinary temperatures. The most universal storage place for fats is the seed, where it is in some cases the dominant form of food, and in almost all it is present in greater or less quantity. The main seeds that contain fats are cotton seed, castor bean, flax, peanut, sunflower, rape, and corn. It is by no means confined to seeds, but occurs in the flesh of fruits (olive), in rhizomes (potato, iris, and sedges), in bulbs (onion), and in roots (carrot). In almost every part of a plant, indeed, small quantities of oil may be found, and from many reservoirs it can be extracted in commercial quantities.

True oils must be distinguished from volatile or essential oils, which are common in leaves and flower parts. The latter usually have a distinct odor and make a temporary translucent spot on writing paper, whereas that made by true oils is lasting.

Accumulated oils are obtained for commercial uses by crushing and pressure; but as only a portion of the oil (which forms 2 to 68 per cent of the dry weight) can be recovered thus, the "cake" remaining, with its residue of oil and other substances, may still be valuable food for animals, as is the case with cotton and flax seed.

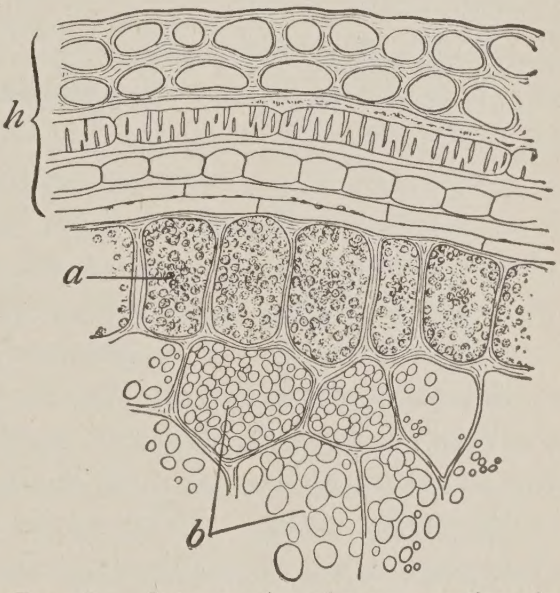


FIG. 48. — Outer portion of a cross section of a wheat grain: *h*, various integuments of the ovary and seed, forming the husk; *a*, cells of "aleurone layer" of endosperm, loaded with protein grains; *b*, starch-bearing cells. — After COBB.

Proteins. — Proteins, unless they take on a specific solid form, cannot readily be distinguished from resting protoplasm. Thus, the "gluten" of wheat is apparently a part of the network of protoplasm in which the starch grains are imbedded. The best known storage forms appear in vacuoles of the endosperm in seeds. The proteins accumulate in the small vacuoles, and upon the loss of water, characteristic of maturation for a resting period, become more and more concentrated, until finally they solidify, forming the "aleurone" or protein grains. These are very commonly associated with reserve starch, either in the same cells, as in the pea

and bean, or the protein grains are characteristic of certain cells, as in wheat and other cereals, where they abound in the outer layer of the endosperm (fig. 48). In large grains some proteins may crystallize out, as in the castor bean (fig. 49) and the Brazil nut, but oftener they remain apparently homogeneous.

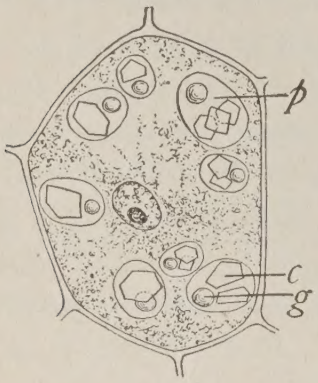


FIG. 49. — Cell from endosperm of castor bean (*Ricinus communis*): *p*, *p*, protein grains, made up of amorphous proteins, crystalline proteins (*c*) ("crystalloids"), and globular compounds of proteins with calcium and magnesium, the globoids (*g*). — Adapted.

Amides. — Amides occur in such quantities, especially in some sappy reservoirs, that they may be considered as stored food. There they may form 40–70 per cent of the nitrogenous materials.

Alkaloids. — Some studies of cacao ("cocoa") and coffee make it probable that their alkaloids (see p. 199), which are of a different type from most, may be a form of surplus nitrogenous food, since they come again into use. They constitute a very compact source of available nitrogen.

Combination of food. — It must not be supposed that the foods above named accumulate independently. On the contrary, they always occur associated, though one form is likely to be dominant. Rarely, if ever, are they so related to one another in amount as to form what animal feeders call a balanced ration. This is shown by the fact that, when growth is resumed, food of one sort is not used in the ratio which it bears to others stored with it. Often indeed the reserves are not exhausted until the plant or shoot, having begun independent manufacture, is able to supplement the deficiencies in the stored ration. Thus, finally, it may utilize all the accumulated reserve, but often this is not done, and the excess is again stored elsewhere.

Traveling forms. — Since the places of storage are seldom the places of food making or use, translocation of food usually precedes and follows storage. Unfortunately, little is known about the translocation of foods. It seems clear that the traveling forms must be relatively simpler than those in which they are stored. Obviously, they can travel only in solution, and, as a rule, the protoplasm does not permit the passage of the foods in their storage forms. Thus, cane sugar probably travels as glucose and fructose; the fats as glycerin and fatty acids or, indeed, the fats may always be converted into soluble carbo-

hydrate before they are transported [1]; the proteins as amino-acids and amides such as asparagin. For in all translocation of foods, whether in small plants or large, it is necessary that they be able finally to diffuse through live cells, and the more complex compounds are usually unable to do this.

Diffusion. — In the smaller plants osmotic differences alone must account for the transfer from cell to cell. This may be facilitated by the delicate protoplasmic connections which commonly exist and would make it unnecessary for all the food to pass through the cell wall itself. In fungi which have coenocytic hyphae, the absence of transverse partitions probably facilitates transfer; while the surging movements that have been observed in the contents of certain molds (Mucorales) would certainly do so. Yet actual knowledge regarding the translocation of food in even the simplest plant is scanty. Food obviously gets from place to place, and there is apparently no way for it to do so except by diffusion.

Conducting system. — In the larger plants a conducting system is developed; and it is evidently advantageous that the slower movement of diffusion be supplemented by a more rapid one along the chief lines of travel when the factories are separated by considerable distances from the places of use or storage. This conducting system in all the vascular plants consists of the phloem strands. It may be supplemented in certain large families by the latex system, though the function of the latex is somewhat uncertain.

The recent suggestion of Dixon,[2] that xylem may carry the foods both upward and downward through the stems, cannot be taken seriously. The experiments on which this suggestion was based were not adequate to demonstrate the downward movement of foods through the xylem. It must be recognized that water can move through the plant in any direction, in response to a saturation deficit; and a partially wilted plant supplied with water at the top will, of course, transmit it downward through the xylem. There is no evidence for the downward flow of foods through the xylem, although it is probable that some soluble foods travel upward through the xylem along with the ascending transpiration stream. Even in winter time the rise of

[1] Rhine, J. B. Translocation of fats as such in germinating fatty seeds. *Bot. Gaz.* **82**: 154–169. 1926.

[2] Dixon, H. H., and Ball, N. G. Transport of organic substances in plants. *Nature* **109**: 236–237. 1922.

water in a tree is rapid enough to prevent the diffusion of sugars or other soluble foods in a downward direction through the woody tissues.

Phloem strands. — The phloem strands are usually definitely related to the xylem strands (which carry water), though they occur also independent of them. In most seed plants there is a phloem strand lying along the outer face of a xylem strand, and except in the monocotyledons there is generally between them a meristem (cambium), which may add to the radial diameter of both xylem and phloem. It may also, if it extend from one strand to another around the axis, produce new secondary phloem strands between the old ones. The phloem strands form a continuous system, and may be traced from the stem outward into the leaves and downward into the roots. So followed, they usually disappear before the xylem strands end; that is, their differentiation does not begin so early in the rootlets nor extend so far in the leaves.

Elements of phloem. — The elements of the phloem strands are sieve tubes, companion cells, cambiform cells, and parenchyma, with sometimes mechanical tissues, though the latter belong more commonly to the adjacent tissue systems. It is impossible to specify the precise rôle of each of the elements; but among them all the sieve tubes may be considered the chief lines of conduction, the others being supplementary thereto.[1] In a way the sieve tubes are analogous to the tracheae of the xylem; particularly in that, having their end walls partially resorbed, they constitute tubes through which the foods may move without the delay necessitated by osmotic transfer from cell to cell.

Evidence of conductivity. — The reasons for assigning conductive functions to the phloem strands are chiefly these: (1) The pith is so commonly dead and its cells filled with gases that it may be excluded from consideration. (2) The cortex, too, is often dead; particularly is this almost universally true of the older parts of shrubs and trees in which it is frequently sloughed off after a few years; yet there is an active transfer of foods. Moreover, the movement of food through the protoplasmic membranes of live cells is apparently too slow to meet the needs of plant growth. (3) When the cortex is removed by surgical operation, the supply of food seems to be quite adequate to permit development; but if the phloem strands are interrupted, transfer of foods is almost or quite stopped.

[1] It is as though the sieve tubes were the main railway lines and the adjacent tissue sidetracks temporarily occupied.

This is particularly noticeable when girdling occurs in nature, as when birds destroy a zone of bark in conifers whose wood remains able to conduct water. The tops and roots (if one or more circles of branches below the injury remain, keeping the latter supplied with food) may continue to live for years (fig. 50), yet the vigorous growth is above the injury. Girdling experiments with willow shoots are often cited as adequate proofs of the conductive function of phloem. For example, by removing a ring of cortex 5 mm. wide, a few centimeters from the lower end in one case and several times as far in another, and placing both shoots in water, lateral roots and shoots develop in both cases. Their vigor is somewhat proportional to the relative lengths of stem below and above the girdling, and this is taken to indicate that the new parts can draw only upon food stored in the part of the stem above and below the girdling, transfer being prevented by the interruption of the phloem. But if bridges of bark be left across the gap, the differences of development tend to disappear; and the more numerous the bridges the less the differences. While such experiments agree fairly well with other observations, they are in themselves not conclusive, since the results are complicated with obscure phenomena of regeneration, and perhaps with wound irritability.

FIG. 50. — Portion of the trunk of a pine, the bark completely destroyed by birds at *a*. A single circle of branches below keeping all the parts lower than *a* scantily supplied with food, the upper part made an excessive growth, especially in the neighborhood of the wound, but food could not pass *a* freely (perhaps not at all). Original in the museum of Purdue University — From photograph supplied by STANLEY COULTER.

(4) The content of the sieve tubes, which is a coagulable slime, consists more largely of foods than would be at all likely unless the sieve tubes were organs of either conduction or storage, and the latter supposition is unlikely because the foods are almost entirely in solution. In a typical case analysis showed that, excluding water, the constituents were: carbohydrates, 30 per cent; amides, 38 per cent; proteins, 20 per cent. So rich a supply of soluble foods could hardly be found anywhere else. (5) A bit of merely corroborative evidence is derived from the distribution and relative development of the phloem. No plants need more facile movement of foods than vines, whose stems are necessarily slender and long, and in none is there better development of the phloem. Indeed, when the anatomist wishes to study the largest and most specialized sieve tubes, vines are almost invariably selected. Moreover, where the requirements for food

transfer are the greatest, as in flower clusters and in the branches of inflorescences, the phloem strands are particularly well developed.

Rhythmic translocation. — Since leaves are the principal regions of food making, which is distinctly rhythmic by reason of the alternation of light and darkness, the translocation of food shows a corresponding rhythm. The transfer of any soluble food is continuous, and the rate is determined by the usual factors; but, as the transportation facilities are overtaxed during the day, there is on the whole an accumulation of food in the leaves then; only after the nightly slackening does emptying of the leaf become obvious.

That a leaf which shows starch near the close of a day may show none in the early morning does not necessarily indicate that carbohydrates have been carried off during the night, though they doubtless are, but only that they have been reduced in amount in some way, probably by migration, by conversion into other foods, and by digestion and use in respiration or building.

Causes of movement. — Nothing is satisfactorily known as to the causes of movement of the foods in the phloem. In the sieve tubes the protoplasmic membranes closing the ends probably retard the rate of diffusion; on the other hand, translocation may be facilitated somewhat by mechanical mixing due to bending and other compression of parts of the system. That the contents are under pressure is shown by the rapid oozing of material from cut sieve tubes, an amount being reported in *Cucurbita* which indicates that one or even two internodes had been emptied, and so the material must have passed 75 to 100 of the sieve plates (the perforate end walls of the sieve cells). The source of this pressure and the effect of it on translocation is not known.

However, it may be very significant, for the movement of the translocated food occurs much as one would expect if it were conducted in a system of tubes under slight pressure, enough to cause movement. The movement is far too rapid for diffusion, and it can occur against the force of gravity, as when the wheat head stores the food sugars coming from the leaves below. In a system of water pipes conducting water under pressure, the water will flow out at any open faucet, wherever it happens to be located, just so it is not too high for the pressure to reach it. And apparently the food travels toward any place where it is being withdrawn from the conducting system, whether it be at the upper end, lower end, or at some intermediate point. The behavior of the conducting system is like that of a system in which the fluids move

under pressure from the place of manufacture to the place of storage. While pressures are known to exist in the phloem, it is difficult to be certain that this pressure can cause significant movement of the food-containing liquid contents. The problem requires careful and searching investigation. It is probable that rotational movement in the protoplasm in the phloem cells aids in the transfer of sugars, but even this assistance to diffusion movement leaves us with an inadequate conception of translocation. In a recent [1] paper it is suggested that the sugars actually travel at about the rate which one would expect if they were in the gaseous state. Even the rotational movements of protoplasm are very sluggish as compared to the rate of gaseous diffusion. We are still far from a satisfactory explanation of the transfer of organic solutes from place to place in the plant body.

Latex system. — In certain families,[2] it may be that translocation of foods takes place through the latex vessels, as well as by the phloem. Latex vessels form a system of branched or anastomosing tubes running through the cortex (more rarely elsewhere), and ending blindly in the leaves and roots. Histologically, they are coenocytes or cell fusions. If coenocytic, they are known as non-articulated latex vessels; but if formed by the end-to-end fusion of cells, the system is an articulated one. They approach very near to the growing points, and in the leaves have close relations with the manufacturing cells, the very arrangement sometimes suggesting its fitness for collecting foods. The latex which fills these tubes is the cell sap of a huge vacuole, the protoplasmic contents being reduced to a very thin layer. Latex is in part a watery solution of many substances, such as proteins, sugars, gums, tannins, alkaloids, and salts; in part an emulsion of oils and tannins in droplets; and in part supended granules of starch, gum, resin, and caoutchouc. Some latex is translucent, but usually it is an opaque, white, yellow, or orange liquid, familiar to many as the milky " juice " of dandelion, poppy, milkweed, or the orange " blood " of the bloodroot. Latex is commercially important as the source of opium and its alkaloids, of India rubber, and of gutta percha. The latex is also present in the plant under pressure, and if utilized at one part of the system, may be transferred to the point of use.

[1] Mason, T. G., and Maskell, E. J. Studies on the transport of carbohydrates in the cotton plant. *Ann. Bot.* **42** : 189–253. 1928.

[2] Particularly the Papaveraceae, Compositae (Cichorieae), Lobeliaceae, Campanulaceae, Asclepiadaceae, Apocynaceae, Euphorbiaceae, Moraceae, Araceae, and Musaceae.

Function. — The principal reasons for ascribing to latex vessels the function of a conducting system are the abundance of foods in the latex, and the peculiar structural relations of the latex vessels to the nutritive cells of the leaves. The carbohydrate and nitrogenous foods of the latex run as high as 30 per cent of the dry matter therein; they are most abundant when active growth and development are beginning, and least so when growth is checked and a resting period is at hand. In some leaves the latex vessels look as though they were favorably arranged to receive materials collected from the nutritive cells. Yet for the conductive function the evidence is rather presumptive than convincing. It may be that the latex has to do rather with storage and protection.

8. DIGESTION

Nature of digestion. — Whenever foods are insoluble in water (as are some of the most valuable ones), they cannot be used by plants until transformed into a soluble substance. Whenever soluble foods are unable to diffuse readily through protoplasmic membranes, they can scarcely move from one point to another, and are available, if at all, chiefly in the cell where they happen to be. Every transformation of food by the agency of a third body from an insoluble to a soluble and from an indiffusible to a diffusible condition, whatever the precise chemical nature of the change, is summed up in the term *digestion*. This use of the term is in exact accord with its long use in animal physiology. The processes in plant and animal, indeed, are essentially the same; they are wrought by the same sorts of agents, affect the same sorts of substances, and result in the same sorts of products.

No special digestive organs. — Plants differ from the larger animals in having no pouched tube wherein food is lodged, and in which some of the more striking digestive processes take place, before the food truly enters the body. This digestive tract, its parts and accompanying glands, constitute the special digestive organs of the animal, though much important digestion takes place elsewhere. Plants have no special digestive organs comparable to these; but places of food making and food storage must be places where digestion is also particularly active.

Misleading comparisons of the leaves to the stomach not rarely occur in primary books, which thus seek to "explain" the work of a leaf. When, as in one notable instance, a leaf is compared to a *kitchen*, where the dilute "soups," coming up from the roots, are "boiled down"; later to a *stomach*,

where the food is made ready; and finally to the *lungs*, by which the dear little plant breathes, the child would have a truly appalling notion of a leaf were he not usually immune to such bad pedagogy, by reason of his ignorance of at least the stomach and lungs.

Extra-cellular digestion. — In plant as in animal, many foods must be digested before they can enter the cells at all, while others are digested as they lie in the cells. So one may distinguish, as to location, extra-cellular and intra-cellular digestion; but agents, processes, and results are essentially alike in both. In a fungus which merely pushes its way among the inter-cellular spaces of another plant, it is impossible to say whether any food is being digested or whether only what is already soluble and diffusible is being used. But when a fungus sends a branch, as a *haustorium*, through the cell wall (fig. 36), or when, as in certain wood-destroying fungi, the mycelium penetrates the walls freely in all directions, it is obvious that by some means the wall is actively dissolved at the point of contact, although, as pointed out previously, fungi may penetrate cell walls by mechanical pressure.

Chemical changes. — The changes characteristic of digestion result in the cleaving of compounds into two or more simpler substances, with the taking up of water. This method of cleavage is called hydrolysis. All digestive changes in foods consist of hydrolyses by which the foods are converted into simpler soluble substances.

Thus when cane sugar is digested:

$$\underset{\text{saccharose}}{C_{12}H_{22}O_{11}} + \underset{\text{water}}{H_2O} \rightleftharpoons \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{fructose}}{C_6H_{12}O_6}$$

Starch when digested takes up water, and four fifths of it breaks up into maltose units ($C_{12}H_{22}O_{11}$), the other fifth resisting full digestion for a long time. The maltose is further digested into two units of glucose, with assumption of another molecule of water. Glucosides also require water for their hydrolysis. Thus sinigrin, a glucoside characteristic of the plants in the mustard family, cleaves thus:

$$\underset{\text{sinigrin}}{C_{10}H_{16}NKS_2O_9} + H_2O \rightleftharpoons \underset{\substack{\text{allyl thiocyanate}\\\text{(mustard oil)}}}{C_3H_5CNS} + \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\substack{\text{potassium-hydrogen}\\\text{sulphate}}}{KHSO_4}$$

In the digestion of fats, the triglycerides are hydrolyzed to glycerol and fatty acids, three molecules of water being required to hydrolyze one molecule of fat.

The proteins are still more complex than the fats, but the process of digestion involves the same kind of chemical change. The long chains of amino-acids, or the substituted diketopiperazide rings, are split up

into amino-acids, the break down always occurring with the incorporation of the ions of water into the molecules.

Digestion is thus seen to involve just one type of chemical change, hydrolysis; and it is just the reverse of condensation, which nearly always involves the loss of water as the complex foods are built up. Digestion reverses the process. Just as condensation usually occurs during times when local or general water deficit exists in the storage regions, so digestion occurs when a plentiful water supply occurs either locally or generally in the storage tissue. A ripening seed condenses food as it dries out slowly; but later, when fully ripened and planted, saturation of the seed in the moist earth leads to a digestion of the reserve food. The relationship between digestion and condensation may be represented by the following reversible reaction:

$$\text{Sugar} \underset{\text{Digestion}}{\overset{\text{Condensation}}{\rightleftharpoons}} \text{Starch} + H_2O \underset{\text{(Imbibition)}}{\overset{\text{(Evaporation)}}{\rightleftharpoons}}$$

When evaporation removes water from the reaction, sugar changes to starch, with loss of water; and when water is imbibed by a starchy endosperm, hydrolysis occurs with production of sugar.

The chemical changes of digestion represent only a few of the multitudinous reactions going on in the plant. The rate of these reactions, like all others, depends on temperature, concentration, etc., and especially on the effect of other substances which are present. It is not always evident just how a third body affects the rate at which one substance is converted into another in a chemical reaction, and so doubtless many effects of this sort pass unnoticed. But when the effect is pronounced, the third body is spoken of as a *catalyst*, and the effect of the catalyst on the reaction is known as *catalysis*. By such agents reactions, so slow as to be unnoticed, may be greatly accelerated and become evident; and others, which might be very rapid, are retarded, even until they are negligible.

The inorganic catalysts, like platinum black, colloidal nickel, and other colloidal metals owe their catalytic properties to their specific surface, and the large number of free valencies of superficially located atoms, which permit addition compounds to form. The interacting substances are absorbed on the surface of the catalyst, and are attracted with such force that the molecules are packed on the surface of the colloidal catalyst. This packing brings the interacting molecules so closely together that chemical reactions occur rapidly that

otherwise would take place only very slowly. Indeed, it is probable that in certain cases the catalyst can initiate reactions that otherwise would not take place at all, although we ordinarily think of a catalyst as merely increasing the rate of a slow reaction.

Enzymes. — Among the catalytic agents (which are varied and not at all confined to living beings) are certain substances produced by organisms and called *enzymes*. These are widely different in their action, though many of them seem to be of protein nature, so far as their chemical character is made out. The great difficulty in determining their chemical character lies in the impossibility, up to date, of separating them from the other proteins of the cell and obtaining them in any certain state of purity. In general they act best within certain narrow limits of temperature, such as 30–45° C., and most are totally destroyed at such temperatures as 60–75° C. Small quantities of free acid or alkali may facilitate their action; while certain metallic ions, *e.g.* Hg, Cu, Ag, may retard or inhibit their ordinary effect, just as they "poison" a live cell.

These enzymes owe their activity partly to their colloidal condition (development of specific surface), and partly to their chemical constitution. Recent discoveries indicate that enzyme reactions may be chemical in nature, and that the enzyme actually unites chemically with the substrate upon which it acts, forming large addition compounds. For instance, in the digestion of sucrose, it is probable that the enzyme sucrase or invertase, and the sucrose and water, all three unite to form a large unstable molecule. When this unstable molecule breaks down, we find the sucrase unchanged, but the sucrose has been changed into levulose and dextrose, while the water has disappeared. The enzyme can then unite with more sucrose and water, and repeat the catalytic hydrolysis over and over.

Chemically, we do not know just what an enzyme is. It may not be a specific chemical molecule in some cases, but rather some part of a molecule, some specific linkage of atoms in some chemical substance. It has been suggested, for instance, that the enol-lactim linkage in protein molecules may act catalytically. This linkage is $-N = \overset{\overset{\displaystyle H}{\displaystyle O}}{\overset{|}{C}}-$, and may serve in some instances to catalyze reactions.[1]

[1] Falk, K. G. *The Chemistry of Enzyme Actions*. 2d ed. pp. 127–136. Chemical Catalog Co. 1924.

Enzymes are easily inactivated by heat, heavy metal ions, specific chemical substances, hydrogen ions, etc.; and inactivation may result either from the adsorption of the inactivating substances, or from a change induced in the chemical linkages involved in enzyme action. A change of the enol-lactim arrangement to keto-lactam, $-\overset{\displaystyle H}{\underset{|}{N}}-\overset{\displaystyle O}{\overset{\|}{C}}-$, by shifting the hydrogen from the O to the N, and changing the position of the double bond, may completely inactivate this linkage and destroy its catalytic power.

There seems to be a great variety of enzymes, each producing an appropriate effect upon certain foods; but others are known which have to do with reactions quite apart from the digestive changes. The *digestive* enzymes, then, are only part of a larger class of bodies, whose number and variety are only imperfectly known.

Sometimes an enzyme will digest only one kind of food substance. Thus invertase may digest only cane sugar, and have no power to hydrolyze maltose, trehalose, or lactose. Similarly trehalase may act upon no other sugar besides trehalose. Such specific correspondence of enzyme and substrate is spoken of as specificity of enzyme action. The relation of enzyme to substance acted upon has been likened to that of a lock and key. The enzyme must fit chemically to the substance it acts upon. Specificity may have nothing to do with the physical shape of the molecules, but at least the enzyme must be able to form the addition compounds with the substrate, or no reaction can occur. Specificity is found most marked among the carbohydrate-digesting enzymes. In comparison with the carbohydrases the fat-splitting enzymes show little specificity. This may be related to the fact that all true fats contain glycerol; and a single enzyme, lipase, by attacking glycerol, may therefore digest all of them. The proteins, too, have just one type of linkage, the peptide linkage, and we find only a little evidence of specificity among protein-digesting enzymes. Each species of plant possesses protease which digests its own globulins more readily than the globulins of any other species of plant, probably.[1] But so far, peptase and ereptase, peptic and tryptic respectively, are the only protein-digesting enzymes commonly found

[1] Blagoveschenski, A. V. On the specific action of plant proteases. *Biochem. Jour.* **18**: 795–799. 1924.

Blagoveschenski, A. V., and Bielozerski, A. N. The specific conditions of action of leaf peptases. *Biochem. Jour.* **19**: 355–356. 1925.

in plants. There must be a number of autolytic protein-splitting enzymes in plants, but they have not been isolated and investigated.

Reversible action. — The action of a number of enzymes is known to be reversible; *i.e.* they not only, under certain conditions, hasten the otherwise imperceptible decomposition of a particular substance into two or more simpler compounds, but also, under other conditions, accelerate the combination of the simpler substances into the more complex one. Indeed, it seems likely that the constructive action of enzymes may soon be shown to be as important as the destructive. This action would be of the greatest importance in the making of complex foods from simpler ones, such as the formation of starch from glucose, of cane sugar from glucose and fructose, of proteins from amido-compounds, etc. But the knowledge of this constructive action is yet very scanty.

Carbohydrate enzymes. — *Diastase* is one of the most important and widespread enzymes. It is found in practically all parts of plants, but especially in leaves and storage organs. It partly digests starch into maltose, and a residue, representing about 20 per cent of the grain, which resists its action for a long time. In the course of decomposition various dextrins are produced by successive cleavage, presently becoming simple enough to be analyzed. The last member of the series breaks into maltose and isomaltose, $C_{12}H_{22}O_{11}$. There are at least two forms (possibly more) of the enzyme, secretion diastase and translocation diastase, differing in the mode of dissolution of the starch grain. The former erodes the surface irregularly, whence narrow canals penetrate the interior, and the grain often falls into fragments; the latter corrodes the grain almost evenly, reducing it gradually in size until it disappears. Secretion diastase is found mainly in the seeds of the cereal grains, while translocation diastase can be most easily isolated from the leaves of plants, although it occurs in all parts of the plant body.

It is probable that what is here called diastase consists of at least two enzymes: *amylase*, which digests starch to a dextrin, and *dextrinase*, which breaks the dextrin into maltose; this, *maltase* (see p. 176), cleaves into glucose.

Invertase, in like manner, can hasten the hydrolysis of cane sugar into two hexose sugars, glucose and fructose.

Trehalase and several other enzymes in fungi attack trehalose and other sugars peculiar to them, and digest them into the hexoses of which they were originally built.

Maltase, an enzyme which is often associated with diastase, carries the process of starch digestion further, cleaving each maltose molecule into two molecules of glucose.

Inulase likewise attacks inulin, breaking it up into levulins and finally into fructose. Perhaps there is here also more than one enzyme at work.

Cytase is responsible for digesting hemi-celluloses (chiefly mannans and galactans) of seeds, while enzymes under the same name, but probably different, have been found in wood-destroying fungi, and have been assumed present whenever a tissue is penetrated by a hypha, or by a more massive member, as in the sinking of the foot of bryophytes into the gametophyte (see *Morphology*, vol. I, p. 108) and in the emergence of branches of roots through the cortex (fig. 52; see also vol. I, p. 250, and fig. 558).

Fat enzymes. — *Lipase* has been found in organs where fats are present, especially in seeds and many fungi. Lipase breaks up fats into their components, fatty acids and glycerin, which are then readily diffusible. An enzyme called esterase has been found which is also capable of digesting fats. It differs from lipase mainly in its solubility.

Glucoside enzymes. — These are common, setting free glucose from many different compounds. *Emulsin*, for example, breaks amygdalin, a glucoside common in peach, almond, and apple seeds, into hydrocyanic acid, glucose, and benzoic aldehyde, thus:

$$\underset{\text{amygdalin}}{C_{20}H_{27}NO_{11}} + \underset{\text{water}}{H_2O} \rightleftharpoons \underset{\substack{\text{benzoic}\\\text{aldehyde}}}{C_7H_4O} + \underset{\substack{\text{hydro-}\\\text{cyanic acid}}}{HCN} + \underset{\text{glucose}}{2(C_6H_{12}O_6)}$$

The so-called " mustard oil " is produced, along with glucose and two other compounds (see p. 171) from sinigrin, a glucoside characteristic of the mustard family. These actions are very rapid, as shown by the formation of the peculiar flavor or pungency almost as soon as the parts are crushed by the teeth and the enzyme thus brought into contact with the glucoside.

The glucosides are divided into two general classes, the α-, and β-glucosides, which differ from one another only in stereoisomeric configuration of the molecule. The one is the mirror image of the other. The β-glucosides are usually hydrolyzed by emulsin, while the α-glucosides are digested by maltase. One can determine to which class an unknown glucoside belongs by determining its digestibility by these two enzymes.

Emulsin is not a single enzyme, but consists of amygdalase and pru-

nase.[1] It occurs in the bitter almond and hydrolyzes amygdalin, the main glucoside of the bitter almond. Amygdalase first splits the amygdalin into sugar and prunasin. Prunasin is another glucoside as it still contains sugar. The prunase then splits prunasin into sugar, benzaldehyde, and hydrocyanic acid.

While maltase is usually said to hydrolyze the α-glucosides, there is some evidence that maltase is always associated with a second enzyme, which has been called alpha-glucosidase. The methods at present in use to prepare enzymes are not sufficiently specific to separate two enzymes of similar properties, and so the maltase preparation can be used to test for α-glucosides, although it may be alpha-glucosidase as an impurity in the maltase which actually carries on the hydrolysis.

Protein enzymes. — Several enzymes are known which digest proteins. In animals their digestion proceeds by two prominent stages: first, the peptic enzymes (*i.e.* those like pepsin of the stomach) convert proteins into peptones, which are soluble and diffusible; second, the trypsin of the intestine converts proteins and peptones alike into amino-acids and other compounds, still more freely soluble and diffusible. At first protein digestion in plants was ascribed to peptic enzymes; later, because of its completeness, it was referred to tryptic enzymes and the presence of peptic enzymes was denied. Now, however, it is possible to distinguish the two classes of enzymes, though they act together and carry forward the processes to completion without a pause at any particular stage of simplification. The peptic enzyme of plants is usually called *peptase*, while the tryptic enzyme is called *ereptase*. They are nearly always associated in the organs where protein digestion occurs.

Inasmuch as the proteins are not prominent among surplus foods, it might seem at first sight that protein digestion was unimportant in plants. But aside from the stored food, many instances where such digestion must occur may be cited. Thus, the exhaustion of proteins to a large extent from the foliage of annuals as the seeds ripen (*e.g.* as shown in cereals), and the partial recovery of proteins from leaves of trees before their fall, presuppose protein digestion. So, also, the action of a plant parasite or saprophyte on animal bodies, and of the curious pitchers and traps of carnivorous or insectivorous plants involve protein digestion.

[1] Armstrong, H. E., Armstrong, E. F., and Horton, E. Studies on enzyme action. XVI. The enzymes of emulsin. (i) Prunase, the correlate of prunasin. (ii) Distribution of β-enzymes in plants. (iii) Linase and other enzymes in *Linaceae*. *Proc. Roy. Soc. London* B. **85** : 359–378. 1912.

Assimilation. — All the digestive changes are preliminary to the translocation of foods from places of manufacture to places of storage or use, or from places of storage to places of use. The use of food may involve a direct oxidation of the soluble sugars, or it may first be built into living tissues of the body which *grows* thereby. This final step in the chemical progress of foods, by which they become a part of the living protoplasm, is known as *assimilation*. To give it a name is about all that can be done at present, for until very much more is known of the chemistry of proteins, of which protoplasm chiefly consists, practically nothing can be known of the details of assimilation.

Metabolism. — The important steps in nutrition are these: (1) the making of carbohydrates in green parts, properly lighted, out of H_2CO_3; (2) varied modification of these and incorporation of nitrogen (often also sulphur and phosphorus) from mineral salts to form amino-acids and finally proteins; (3) the assimilation of proteins into protoplasm. On the whole these steps are upward; the material becomes, though with many fluctuations, gradually more and more complex, until it enters upon its final, most complex, least stable, living condition. It is maintained for a time at the high level as living stuff, or it becomes a part of some more permanent portion of the body, like the cell wall; or it is broken up and reduced gradually to simpler compounds, some perhaps to be rebuilt into living matter again, some to break into simpler and simpler compounds and to leave the body (*e.g.* as CO_2, H_2, etc.).

Metabolism is an old general name for *all* the chemical changes in a living organism. The constructive phases of nutrition are often summed up in the term *anabolism* or constructive metabolism; the destructive phases as *catabolism* or destructive metabolism. In the former the processes tend to be synthetic; in the latter analytic. Having considered the synthetic processes, the analytic ones demand attention in the next chapter.

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CHAPTER IV. — DESTRUCTIVE METABOLISM

1. RESPIRATION

Respiratory organs. — The word *respiration*, or its English equivalent, breathing, suggests at once the currents of air into and out of the lungs, and the bodily movements that cause them. The reason for this is that so much attention has been given to these matters in human physiology that the more important processes, which take place in the muscles and live tissues generally, have been almost ignored. This is emphasized by the fact that the phrase " respiratory organs " means the lungs and the air passages thereto, while the blood, which is an equally important adjunct to the aëration of the tissues, is not usually included. But air passages, lungs, chest wall, diaphragm, blood vessels, and blood, not to mention others, are all necessary organs. The fundamental processes, however, take place in the living cells; and they go on there, for a time at least, whether or not, by accessory mechanical means, the oxygen of the air is supplied and the waste products removed.

Since in plants the accessory organs are very simple indeed, their structure and behavior need little consideration, particularly as they are at the same time, in green plants, related to transpiration and to photosynthesis (see aërating system, p. 53). So botanists have focused attention upon the essential processes in respiration. This difference in emphasis has tended to obscure the fundamental likeness of this function in plants and animals.[1]

Identical in plants and animals. — Excluding the processes of aëration, respiration in plants and animals is alike in all essentials. When the likeness of the living matter in the two is considered — a likeness so great that neither microscopic observation nor analysis can distinguish them by structure, behavior, or composition — the

[1] It has been proposed to retain the term *respiration* for the aërating processes, and to use the term *energesis* for the chemical changes in the tissues, whose end seems to be the setting free of *energy*. The present tendency, however, is to regard respiration *not* as a process of aëration, but as an energy-releasing process. The term energesis has not made a place for itself in physiological literature.

fundamental identity is not surprising. Yet popularly it is widely believed that the respiration of plants, or of green plants at least, is exactly the reverse of that of animals. This misconception is due to confusing the effect produced upon a limited volume of air by the respiration of animals and by the photosynthesis of plants, two processes which are as little comparable in their results as are walking and eating.

Neither gaseous exchange nor combustion. — The striking change that most organisms produce in the air of a limited space is the reduction in the amount of oxygen and the increase in the amount of carbon dioxide. This can readily be demonstrated by putting a considerable quantity of germinating seeds or opening flowers into a fruit jar and sealing it for a few hours. On then lowering a lighted taper into the jar, the flame will be extinguished; and a cup of baryta water if lowered into the jar will be covered quickly with a film of barium carbonate. This has led to a superficial conception of respiration, current in textbooks and encyclopedias, as an exchange of the gases, oxygen and carbon dioxide, between the air and the organism. Because in the burning of wood and other carbon compounds oxygen is consumed and carbon dioxide is produced, respiration has been assumed to be a process of oxidation, in which foods undergo "combustion" in the same sense as the fuel in a furnace, the energy being liberated as heat and in other forms, when the carbon of the compounds is combined with the oxygen of the air. One striking difference between "combustion" inside an organism and outside is that the former occurs at low temperatures, while the latter takes place commonly at high temperatures. To escape this difficulty the term "physiological combustion" was invented. But the conception of respiration as an exchange of gases accompanying oxidation of carbonaceous foods is inadequate, and comparing it to any sort of combustion is more misleading than helpful.

Aërobic and anaërobic respiration. — In the first place, though ordinarily oxygen is fixed, oxygen is not indispensable to respiration; and in the second place, though ordinarily CO_2 is evolved, carbon dioxide is not a necessary product and probably in no case does the O_2 combined with the C come directly from the air. That being so, it is obvious that the above-mentioned conceptions as to respiration cannot be valid. That respiration sometimes goes on in the absence of free oxygen, makes it necessary to distinguish normal or *aërobic* respiration

and intramolecular or *anaërobic* respiration.[1] Aërobic respiration proceeds only when O_2 is present in sufficient quantities, and among the end products two, CO_2 and H_2O, are characteristic, though formed in very variable quantities in proportion to the O_2 taken up. Anaërobic may replace aërobic respiration in any organism when O_2 is cut off, and may proceed for a long time; but the end products are various and quite different from those of aërobic respiration. Among them are commonly ethyl alcohol and hydrogen, and less CO_2. Certain minute organisms may pass their whole existence without oxygen, which indeed hinders or altogether stops their development, and they are thus restricted to anaërobic respiration. In most organisms, however, anaërobic respiration can be considered only as a makeshift.

Nature. — What then is the fundamental feature of a process that goes on under such different conditions and results in such diverse products? It is clear that all organisms, all cells, all living parts of cells, are dynamic, and perform work. Energy is required for all work performed in the living cells, whether the work is growth, or movement, or food storage, or digestion, or any other kind of cellular or organic activity. Aside from radiant energy, used in photosynthesis, the organism makes use mainly of chemical energy. All complex food substances, and living protoplasm itself, contain potential chemical energy which can be released or set free in kinetic form only by the breakdown or simplification of these substances. The essential feature of this breakdown seems to be *energy release*, which is accomplished through oxidation-reduction reactions which occur everywhere in the living cells of the organism. The release of energy from complex organic substances by oxidation-reduction reactions intimately associated with the living protoplasm is the process of respiration. Respiration then may be defined as the release of energy through the oxidation of complex organic substances, the energy appearing in such a form that the organism can use it in doing work.

The main substance decomposed in this way is glucose, although many other compounds must also undergo respiratory changes in the protoplasm. Even protoplasm itself suffers some decomposition which yields energy for work.

[1] Inasmuch as under the conditions one is as really *normal* as the other, and as the term *intramolecular* expresses an interpretation of anaërobic respiration which is no longer tenable, the words *aërobic* and *anaërobic* (*aer*, air; *bios*, life; *an*, not), applied first to organisms that live in air or flourish only when it is excluded, are preferable.

Anaërobes and aërobes. — Those organisms whose oxidation-reduction reactions do not involve the use of atmospheric oxygen, but rather the splittings of compounds in such a way that part of the carbon is more completely oxidized, are called anaërobes, that is, organisms which respire without atmospheric oxygen or air. When, however, the oxidation-reduction reactions involve the use of free oxygen, we call the organisms aërobes. Ordinary green plants are facultative aërobes; that is, they *can* live if they must, for a time, anaërobically. But usually, and under normal conditions, they are aërobic. Many bacteria also, such as the nitrification and nitrogen fixation bacteria, are aërobes. But some bacteria are anaërobes. *Bacillus tetanus* and *B. denitrificans* are examples of anaërobic bacteria.

If the organism dies when deprived of oxygen, it is an obligate aërobe; if it dies when given oxygen, it is an obligate anaërobe. Those that normally live without oxygen, but can live as aërobes if necessary, are called facultative anaërobes. And those that ordinarily use O_2, but can live without it temporarily, may, like our higher plants, be called facultative aërobes. Practically all of our higher plants can, when deprived of oxygen, respire anaërobically for a time, but finally die if given no oxygen at all.

The obligate anaërobic bacteria, which die in the presence of oxygen, are interesting forms. It has now been demonstrated that some of these, possibly all of them, are peroxide formers.[1] They cannot form peroxide while oxygen is absent. But when given O_2 they form H_2O_2 within their bodies, and this substance is so toxic that it kills them. This satisfactorily explains their sensitiveness to traces of oxygen.

Anaërobic respiration and fermentation. — Anaërobic respiration and fermentation are identical, except that fermentation includes other processes concerned with the nutrition of the organisms, in addition to respiration. They are incomplete oxidations, in which some of the breakdown products accumulate. Alcoholic fermentation is the result of the anaërobic respiration and nutrition of the yeasts. Lactic acid fermentation is the result of anaërobic respiration and nutrition of *Bacillus acidi lactici* and seven or eight other similar bacteria. Acetic acid fermentation is the result of the respiration and nutrition of *Mycoderma aceti*, or "mother of vinegar."

[1] McLeod, J. W., and Gordon, J. Further indirect evidence that anaërobes tend to produce peroxide in the presence of oxygen. *Jour. Path. Bact.* **28**: 155–164. 1925. See also **25**: 139–140. 1922.

Some free oxygen is used in this case. Butyric acid fermentation is the result of anaërobic processes of respiration and nutrition of *Clostridium butyricum* and other butyric acid organisms. We shall consider each of these fermentations briefly.

2. FERMENTATION

Alcoholic fermentation. — The alcoholic fermentation is produced in different sugars by various organisms. The sugars that are now known to be fermentable are only those the number of whose carbon atoms is 3 or a multiple of 3; thus, the trioses ($C_3H_6O_3$), hexoses ($C_6H_{12}O_6$), and nonoses ($C_9H_{18}O_9$) are directly attacked; while the more complex carbohydrates (di- and polysaccharides), such as cane and malt sugar ($C_{12}H_{22}O_{11}$) and starch [$5n(C_6H_{10}O_5$], are usually fermented only after they have been simplified by cleavage into hexoses. Some recent evidence indicates that some of the di-saccharides may be fermented directly, without previous hydrolysis. This seems to be true for maltose, cane sugar, and lactose. Why this limitation of fermentation to the 3, 6, or 9 carbon sugars exists, and why within this there are other limitations even more specific, is not known. The organisms concerned are chiefly those known as yeasts (Saccharomycetes), but certain molds and bacteria also give rise to ethyl alcohol, though the latter more commonly produce higher alcohols (propyl alcohol, butyl alcohol, etc.). In this connection it is to be remembered that even the higher plants produce ethyl alcohol in the course of anaërobic respiration, a very significant fact.

The sugar is split up in large measure into CO_2 and ethyl alcohol, but there are other products, such as glycerin, succinic acid, etc., in smaller quantity. Fermentation proceeds very slowly when the yeasts are abundantly supplied with O_2; then, however, they grow and multiply rapidly, and apparently use the sugar chiefly as food. But when the supply of O_2 is small, so that their vegetative processes are hindered, fermentative action is increased. Though alcohol is produced at all times, its quantity is in a sort of inverse ratio to the favorableness of the conditions for life. When 12 per cent have accumulated in the liquid, the action is retarded, and by 14 per cent it is stopped.

Fermentation by yeasts was long believed to be due to the direct action of their protoplasm on the sugar; now it has been proved that an extract, made by grinding the yeast with sand and filter-

ing the juice under high pressure through porcelain, can produce the same effect. The active substance, known as *zymase*, is soon destroyed, unless protected from digestion by accompanying enzymes. Similar substances have been isolated in higher plants, which are believed to act upon carbohydrates in anaërobic respiration,[1] giving rise to alcohol and CO_2 in the same proportions as in fermentation.

Harden and Young showed that zymase is not able to ferment sugars unless it is accompanied by another substance which has been called co-zymase. This coenzyme is heat resistant, and can be separated from zymase by filtering. The zymase remains in the filter, while the coenzyme passes through the filter. Neither the zymase nor the coenzyme can work at the fermentation alone; but when they are brought together, they cause the fermentation to occur. The exact nature of the co-zymase is still not known.

At the same time Harden and Young studied the relation of phosphoric acid to the process of alcoholic fermentation. In the presence of phosphoric acid, or acid phosphates, the rate of fermentation is greatly increased. It is believed that the phosphoric acid enters into combination with the sugars, probably under the influence of an enzyme called phosphatase. In the form of hexose-phosphate (fructose-diphosphoric acid), the sugar breaks down to the three-carbon stage, and finally to CO_2 and C_2H_5OH. The reactions representing the formation of the hexose-phosphoric acid ester during fermentation may be written as follows:

(1) $2\ C_6H_{12}O_6 + 2\ Na_2HPO_4 + \text{zymase} \longrightarrow$
$2\ CO_2 + 2\ C_2H_5OH + C_6H_{10}O_4(Na_2PO_4)_2 + 2\ H_2O + \text{zymase}$

(2) $C_6H_{10}O_4(Na_2PO_4)_2 + 2\ H_2O \longrightarrow C_6H_{12}O_6 + 2\ Na_2HPO_4$

These formulas indicate that two molecules of sugar, two molecules of acid phosphate, and the zymase molecule unite to form some sort of complex addition product, which, upon being decomposed, yields some carbon dioxide, alcohol, water, and the fructose-diphosphoric acid ester. In the second reaction the ester is hydrolyzed under the influence of phosphatase, with the formation of one molecule of free sugar, and the liberation of the phosphoric acid, which can then enter

[1] The source of these carbohydrates is uncertain. They may be either the unassimilated carbohydrates of the food; or, equally well, a carbohydrate nucleus from the decomposition of the protoplasm.

the reaction a second time. The zymase is also liberated during the reaction, so that it can react again.

Other suggestions have been made. Neuberg thinks that the hexoses break down to pyruvic aldehyde ($CH_3—CO—CHO$) in the primary stages of cleavage. This does not necessarily conflict with the idea of hexose-diphosphoric acid ester formation during the process of fermentation, but merely shows an intermediate stage between hexose sugar and CO_2 and C_2H_5OH.

The economic uses of alcoholic fermentation are many. It plays a prominent rôle in the lightening of bread, in which, however, other organisms share with yeast the production of the gases that raise the dough; it is the source of commercial ethyl alcohol, which is distilled from fermented liquids, in which hexose sugars are first produced from corn and potato starch; it gives rise to the alcohol in a host of fermented liquids.

Lactic fermentation. — The lactic fermentation, giving rise to lactic acid, is best known in the souring of milk, and may be produced whenever lactose is present in a solution to which the lactic acid bacterium has access. The main lactic acid organisms are *Bacterium lactis acidi* and *Streptococcus lacticus*. As in the alcoholic fermentation, the accumulation of the products brings the action to a standstill. When 8 per cent of lactic acid has accumulated (or less in milk), the bacterium becomes inactive.

The fermentation consists essentially of splitting the sugar molecule into two molecules of lactic acid:

$$C_6H_{12}O_6 \longrightarrow 2\ CH_3 \cdot CHOH \cdot COOH$$

Acetic fermentation. — The acetic fermentation is due to bacteria, which oxidize ethyl and other alcohols to acids. The commonest form converts ethyl alcohol into acetic acid, $CH_3 \cdot CH_2OH + O_2 \rightleftarrows CH_3 \cdot COOH + H_2O$. In the quick process for the manufacture of vinegar, in which this fermentation is applied, dilute alcohol (6–10 per cent) is allowed to trickle over beech shavings in a deep vat, which have become covered with a slimy coating of the organisms. By the time the alcohol has reached the bottom it has been oxidized completely to acetic acid.

Butyric fermentation. — Butyric fermentation, by which butyric acid is produced from various sugars, especially lactose, and indirectly from polysaccharides, through the agency of bacteria, underlies the production of desirable flavors in butter and cheese.

The reaction involves production of hydrogen and CO_2, as well as butyric acid:

$$C_6H_{12}O_6 \longrightarrow 2\ H_2 + 2\ CO_2 + CH_3 \cdot CH_2 \cdot CH_2 \cdot COOH$$

In most cases there are several reactions running along together, and these formulas represent only a part of what is happening. Other products arise, such as succinic and other acids, and the processes are no doubt very complex.

Putrefactions. — The putrefaction of proteins is wrought by various bacteria, but little is known of the details. Among the numerous end products are the disagreeable gases hydrogen sulphide, mercaptans, skatol, etc.

So a multitude of fermentations might be named, each concerned with a particular compound and due to a particular organism. By the single or successive action of such organisms, complex organic matter is gradually reduced to simple forms, like those from which it was constructed, which then may enter again into the cycle and be built up, through the agency of green plants, into foods.

Significance of fermentation. — Fermentation is to be looked upon as simply the more or less anaërobic respiration of organisms which seem confined to this method of securing energy for their life processes. It is a wasteful method of securing energy, for a large amount of food supplies must be used to secure a small amount of energy. Thus, a gram-molecular weight of grape sugar (the molecular weight in grams, 180 grams) yields about 673 large calories if burned or if respired aërobically. But when respired anaërobically by yeasts, the alcohol produced still contains 652 large calories of heat. The amount set free, then, is only 21 large calories. Aërobic organisms obtain more than thirty times as much energy from the same amount of food as the anaërobic ones do, in the case of alcoholic fermentation. Nevertheless, the anaërobic forms of life secure enough energy by this inefficient respiration to carry on all their life processes, grow, and reproduce themselves. That is all that is needed for successful life.

Cause of anaërobiosis. — Whether an organism must live anaërobically or aërobically depends to a large extent upon the enzyme equipment of the organism. The main anaërobic enzymes are zymase, reductase, carboxylase, deaminase, etc., while the aërobic enzymes are represented by the oxidase system with at least two enzymes, oxygenase, and peroxidase. Catalase is associated with the respiratory

mechanism,[1] but its function is not well understood. Some investigators have attempted to assign it important dynamic functions in the life of the cell, but this is unwarranted by the known facts. Anaërobes usually have the first of these groups of enzymes well represented in their tissues, while aërobes have both groups of enzymes present.

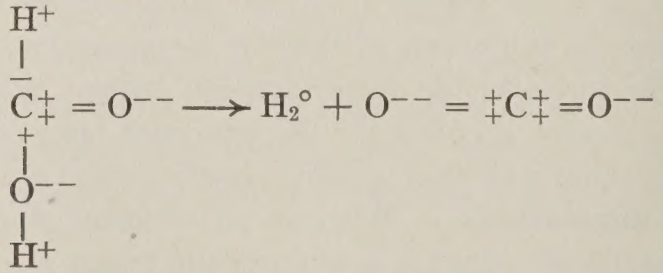
Respiration begins about the same way in anaërobes and aërobes. Zymase splits sugars to alcohol in both. Carboxylase and reductase are at work in both types of organisms. But in the organisms that have only anaërobic enzymes, the process ends with the splitting of compounds. In the aërobes, however, the process goes farther. The products of the anaërobic splitting of sugars, etc., are oxidized by the use of free atmospheric O_2 under the influence of the oxidase system.

Process of respiration. — To understand the nature of the process we must examine some of the possible chemical reactions of respiration. We will begin with the anaërobic processes. Several types of anaërobic breakdown occur, such as direct splittings, breakdown involving use of water as a source of oxygen, dehydrogenations, destruction of the carboxyl group of acids, and splitting out the amine groups of amino-acids as ammonia.

Catalytic splittings. — To illustrate this type of breakdown we will take formic acid. It easily decomposes through the agency of catalysts.

$$HCOOH \longrightarrow H_2 + CO_2$$

This decomposition oxidizes the carbon, and reduces the hydrogen. In formic acid, the carbon has three of its bonds positive, and one negative, as shown in the electrical formula, but in CO_2 all four bonds are positive. The hydrogen changes from positive to neutral, being thereby reduced to gaseous form.



[1] Appleman, Charles O. Relation of oxidases and catalase to respiration in plants. *Amer. Jour. Bot.* **3**: 223–233. 1916. See also Rhine, Louisa. Divergence of catalase and respiration in germination. *Bot. Gaz.* **78**: 46–67. 1924.

Crocker, W., and Harrington, G. T. Catalase and oxidase content of seeds in relation to their dormancy, age, vitality, and respiration. *Jour. Agr. Res.* **15**: 137–174. 1918.

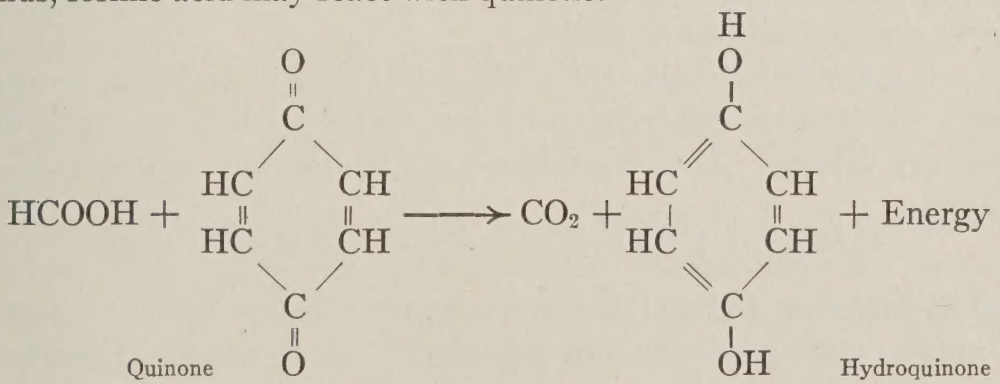
In other words, each hydrogen has taken an electron out of the formic acid molecule, ultimately from the negative carbon linkage, which is thereby changed from negative to positive by loss of the two electrons. All anaërobic respiration involves such transfers of electrons from atom to atom. The atoms that lose electrons are oxidized, those that gain them are reduced. In this particular case energy happens to be absorbed[1] as the H_2 contains more energy than the HCOOH, but energy release always accompanies these changes in the living organism and constitutes the essential feature of true respiration.

Reactions with water. — Acetaldehyde can be oxidized to acetic acid through the agency of catalysts, with release of energy.

$$CH_3 \cdot CHO + H_2O \longrightarrow CH_3 \cdot COOH + H_2 + \text{Energy}$$

Here again the carbon atom of the aldehyde group, $-CHO$, is not as completely oxidized as it is in $-COOH$. In the former the carbon has two negative bonds, in the latter group only one. The carbon has lost two electrons. The oxygen used here was not free oxygen. No air is needed for the reaction. Other substances in the plant besides water contain oxygen, and such supplies of oxygen are often called upon in plants, especially in anaërobic respiration. This may account for the fact that seeds of aquatic plants, like water plantain and rice, can germinate in water which has been freed of dissolved O_2.[2]

Dehydrogenations. — During anaërobic respiration, hydrogen is often disengaged from the molecules undergoing breakdown, but it is not set free in measurable quantity during the process. It is probably taken up immediately by some other compound that readily unites with hydrogen. Such compounds have been called hydrogen acceptors. Thus, formic acid may react with quinone.



[1] Based on facts regarding the heat of combustion of H_2 and HCOOH. Physical chemistries give the value of 68400 for H_2; the International Critical Tables give 62800 for HCOOH.

[2] Crocker, W. Germination of seeds of water plants. *Bot. Gaz.* **44**: 375–380. 1907.

The H_2 cut off from the formic acid is accepted by the quinone which becomes hydroquinone. Again it is seen that the carbon of the formic acid is completely oxidized to carbon dioxide, and energy is released.

In plants, the enzyme reductase acts as a catalyst to remove the H_2 from respirable compounds, and certain pigments, called by Palladin respiratory pigments, serve as the hydrogen acceptors. When these pigments take up hydrogen, they become colorless, and are then known as respiratory chromogens.[1]

If we represent the hydrogen-containing compounds as RH_2, and the hydrogen acceptors as A, we can write the generalized reaction thus:

$$RH_2 + A \longrightarrow AH_2 + R + \text{Energy}$$

Carboxylase reactions. — The enzyme called carboxylase acts on the carboxyl group, $-COOH$, of some of the organic acids, splitting CO_2 out of it. Thus pyruvic acid is converted into acetaldehyde, with liberation of energy.

$$CH_3 \cdot CO \cdot COOH \longrightarrow CO_2 + CH_3 \cdot CHO + \text{Energy}$$

The carbon of the $-COOH$ group is completely oxidized to CO_2 by this change. Just how widely carboxylase occurs, and how general its action is on organic acids is not known with certainty. Some of the alkaloids are decarboxylated amino-acids.

Deaminase reactions. — Deaminase splits the nitrogen from amino-acids as ammonia. These reactions were discussed under nitrification.

$$CH_3 \cdot CHNH_2 \cdot COOH + H_2O \longrightarrow CH_3 \cdot CHOH \cdot COOH + NH_3 + \text{Energy}$$

The ammonification bacteria obtain their energy for life processes by this or similar deaminase reactions.

Some investigators believe that all of the CO_2 set free during respiration is the result of anaërobic processes, water possibly providing the necessary oxygen. Thus one might write the reaction with glucose as follows:

$$C_6H_{12}O_6 + 6\ H_2O \longrightarrow 6\ CO_2 + 12\ H_2 + \text{Energy}$$

The hydrogen set free in this reaction would be taken up by hydrogen acceptors, represented by such substances as quinone and Palladin's respiratory pigments.

[1] Palladin, V. I. Die Verbreitung der Atmungschromogene in den Pflanzen. *Ber. d. bot. Ges.* **26** *a*: 379–389. 1908. See also **26** *a*: 389–394. 1908.

Aërobic respiration. — In the later stages of respiration, the products of the splittings produced by the action of zymase, reductase, carboxylase, deaminase, etc., are completely oxidized by use of atmospheric oxygen. If we assume that all of the carbon was oxidized in the anaërobic processes, an assumption not yet justified by our knowledge, we would have only H_2 to oxidize, — the H_2 taken up by the hydrogen acceptors. The aërobic phase of respiration could then be written:

$$12\ AH_2 + 6\ O_2 \longrightarrow 12\ H_2O + 12\ A$$

Here we see that the acceptors, A, are freed of the H_2, and are now ready to take up H_2 once more as reductase splits off hydrogen from the compounds being respired. In this last phase of respiration, atmospheric O_2 is used, and the oxidase system is supposed to function as the catalyst in providing oxygen to the living cell.

The oxidase system. — This system is made up of three parts, (*a*) an oxidizable body; (*b*) oxygenase; and (*c*) peroxidase.

The oxidizable body may be either autoxidizable or it may oxidize by catalysis. Glutathione, a sulphur-containing body related to cystine, is autoxidizable. It was discovered in 1921, and is considered by some to be important in respiration. On the other hand, there are present in plants catechol-like bodies, related to phenol (carbolic acid), which are oxidizable by catalysis. The enzyme which is supposed to oxidize these catechol-like phenols is called oxygenase or phenolase. The phenols, by taking up oxygen from the air, are converted into organic peroxides which are somewhat unstable, and easily decomposed. The peroxides are then split up by another enzyme called peroxidase, the oxygen being set free in a form that readily oxidizes the H_2 attached to the hydrogen acceptors. This oxygen from the organic peroxides may also oxidize some carbon, for there seems scarcely sufficient reason for believing that all of the CO_2 of respiration is set free anaërobically.

The net result is, that in aërobic respiration both the carbon and hydrogen are completely oxidized, and CO_2 and H_2O are the end products. This yields all of the available energy contained in the respired compound, and produces a high level of energy for work.

All respiration seems to start anaërobically, but it goes to completion only in the aërobic forms of life.

The oxidases. — A number of oxidases[1] have been described. Laccase is the most widespread, and our commonest oxidase. Tyrosinase occurs in the potato, and acts on the amino-acid, tyrosin, producing black melanic compounds. Black heart of the potato[2] is related to this reaction, which occurs after the central cells have been killed by high temperature, freezing, suffocation, etc. Maloxidase has been described from the apple. It readily oxidizes tannin in apples, and turns the flesh brown after bruising. Spermase is found in barley embryos, olease in olives, and luciferase in such plants as have power to produce phosphorescent light. Just how these oxidases are related to one another and how they differ have never been worked out.

Respiratory loss of weight. — The observation has often been made that plants grown in darkness lose some of their dry weight. If one weighs a dry grain of corn or rice, puts it to germinate in darkness, and allows it to grow for a few days in complete absence of light, then if the seedling is dried out again to air-dry condition it weighs considerably less than the original seed. The loss of weight in the case of carbohydrate-high seeds and seedlings is usually somewhat greater than the loss produced by loss of carbon in the form of CO_2, for there is also loss of weight due to the formation of metabolic water[3] during respiration. The loss in weight is therefore due to two causes, loss of carbon and loss of hydrogen, both of which are oxidized during respiration.

Fatty seeds are exceptional in their behavior. Thus seeds of *Xanthium* contain a high percentage of oil, and when grown in darkness for several weeks the seedlings have within a few milligrams of the same dry weight as the original seed. The reason for this peculiar behavior rests in the fact that the plant in its growth is changing fats to carbohydrates in order to build cell walls for the growing plant. The fatty food contains very little oxygen, while the cellulose walls of the thousands of cells produced during growth contain a great deal of oxygen which was absorbed from the atmosphere. The gain in oxygen very nearly equals the losses of carbon and hydrogen during

[1] Kastle, J. H. The Oxidases. *Pub. Health and Marine Hosp. Service U. S. Hyg. Lab.* Bull. **59**. 1909.

[2] Bennet, J. P., and Bartholomew, E. T. The respiration of potato tubers. *Calif. Agr. Exp. Sta. Tech. Paper* No. 14. 1924.

Davis, Ward B. Physiological investigation of black heart of potato tuber. *Bot. Gaz.* **81**: 323–338. 1926.

[3] Babcock, S. M. Metabolic water: its production and rôle in vital phenomena. *Wisconsin Agr. Exp. Sta. Res.* Bull. **22**. 1912.

respiration, so that growth in darkness in the case of fatty seeds is accompanied by relatively very small losses in dry weight.

When plants grow in sunlight, photosynthetic production of sugars and starch from CO_2 and H_2O offsets respiratory loss of dry matter. If photosynthesis builds faster than respiration tears down, there is weight increase. But if respiration exceeds photosynthesis, as might happen on a dull day, or in a plant with a very large root system and a very small leaf area, there is loss in total weight. If the two processes, respiration and photosynthesis, exactly compensate one another, there might be no change in total dry weight, although the plant might be growing in size by increase in the size of vacuoles from osmotic intake of water.

Heat of respiration. — Respiration is an oxidation, and releases energy, some of which is degraded to the form of heat. The heat produced within the tissues of the plant is seldom observable, unless means are taken to prevent the dissipation of the degraded energy into the surroundings. To demonstrate the production of heat, one can place a mass of germinating seeds in Dewar flasks or thermos bottles and compare the temperature of a mass of living seeds and seedlings with the temperature of a like mass of dead sterilized seeds. At the start of the experiment, the temperature is the same in both masses. But the living seeds soon begin to show a rising temperature from the heat of respiration. The temperature difference becomes greater day by day, for the dead sterile seeds remain at the same temperature as they had at the start, while the living seeds become warmer and warmer. Using sterilized seeds of lupine a difference of nearly 30° C. was found by the methods mentioned when the seedlings were about one week old.[1]

Sometimes inflorescences show increased temperatures due to rapid respiration during the opening period. Such inflorescences as the calla lily, whose flowers are borne on a spadix inclosed in a spathe, may show a rise in temperature of 5 to 10° C. above their surroundings at the time of most rapid metabolism. The production of heat by respiration is a continuous process, wherever respiration occurs; but the rate of heat production varies with many different conditions. It is said that a kilogram of seedlings may produce enough heat per minute to warm 1 gram of water from 0 to 50° or even 100° C. Yet, under ordinary circumstances this heat is readily dissipated and the seedlings do not seem warmer than their surroundings.

[1] Peirce, G. J. The liberation of heat in respiration. *Bot. Gaz.* **53**: 89–112. 1912.

When moist plants or manures are piled up, very high temperatures may be produced in the midst of the mass by the combined activities of many different fungi and bacteria. Spontaneous combustion has been caused by such accumulation of heat in damp hay, etc. The heating which occurs in piles of vegetable débris may suppress or kill off all species except those which are especially adapted to live at high temperatures. Such organisms are called thermophiles,[1] and they may show optimum development at temperatures of 55 to 65° C.

Respiratory ratio. — The ratio of CO_2 produced during respiration to the amount of oxygen absorbed is called the respiratory ratio, or respiratory quotient. The numerical value of the respiratory ratio, CO_2/O_2, depends upon several factors, mainly on the kind and quantity of each kind of food being consumed, and on the kind of metabolic processes occurring within the tissues during respiration.

When carbohydrates only are being consumed, theoretically the value of the ratio should be 1. This is indicated by the equation,

$$C_6H_{12}O_6 + 6\ O_2 \longrightarrow 6\ CO_2 + 6\ H_2O$$

which shows that the number of molecules of oxygen absorbed, and of CO_2 produced, are equal.

When the organism completely oxidizes a fat molecule, the respiratory ratio is considerably less than 1. This can be illustrated with tristearin.

$$2\ C_{57}H_{110}O_6 + 163\ O_2 \longrightarrow 114\ CO_2 + 110\ H_2O$$

In this case, the value of CO_2/O_2 is almost exactly 0.7, instead of 1. Similar results would be obtained with a protein, in which the ratio stands between 0.7 and 1.

If organic acids, like malic acid, were respirable, the ratio for such an acid would be above 1.

$$COOH \cdot CHOH \cdot CH_2 \cdot COOH + 3\ O_2 \longrightarrow 4\ CO_2 + 3\ H_2O$$

It is seen that the ratio here is 1.33, and similar ratios would be obtained for any substances more completely oxidized than the carbohydrates to start with. The foods being used by the plant at any given time may vary, but since glucose is the main respiratory sugar, the ratio is often near 1. If it runs below 1 somewhat, the plant may be using some fats along with carbohydrates, so that the average falls below 1.

[1] Noack, Kurt. Die Betriebstoffwechsel der thermophilen Pilze. *Jahrb. wiss. Bot.* **95**: 413–466. 1921. See *Bot. Gaz.* **73**: 419. 1922.

Or, if by photolysis malic acid is being broken up to form some CO_2, the ratio might go above 1, especially if something interfered with the immediate utilization of the CO_2 in photosynthesis.

The kind of metabolic processes that accompany respiration may also affect the value of the respiratory ratio. Sometimes the ratio falls below that normal for fat respiration, even to 0.5–0.6 on occasion. This can be accounted for if it can be shown that the fats are being converted into carbohydrates, rather than undergoing complete respiration. For under this circumstance, oxygen intake would increase without a corresponding increase in CO_2 output. This would decrease the value of the respiratory ratio. In case fats are converted into cellulose, the respiratory ratio for this process is probably about 0.27; and if about the same amount of fat was being used for respiration as for cellulose formation, the average ratio would be almost exactly 0.5. The respiratory ratio, then, may give one valuable clues to the metabolic changes occurring in the plant; but it is mainly determined by the kinds of foods actually respired.

Factors influencing respiratory rate. — Many environmental conditions modify the rate of respiration. Among these factors may be mentioned temperature, light, mineral nutrient and organic food supply, presence of toxic or stimulatory substances, oxygen pressure, etc. In addition to these factors, the age of the organs, current rate of growth, and hereditary qualities may have much to do with the specific rate of respiration shown by any particular plant or organ.

Quantitative determination of respiration rates. — Most frequently the amount of respiration occurring in a given time is determined by measuring the amount of CO_2 given off. This may be done by drawing a current of CO_2-free air through the respirometer chamber, and into a standard solution of sodium hydroxide. The latter absorbs the respiratory CO_2, and is partly neutralized. The degree of neutralization may then be determined by titration of the base; and from the titration, the amount of CO_2 set free in respiration can be calculated.

Another method involves the respiration of plant tissues within an inclosed chamber. The analysis of the gases surrounding the respiring tissues will show how much oxygen has disappeared, and how much CO_2 has been produced. From the known changes in composition of the atmosphere, volume of the chamber and respiring matter, temperature, pressure, and humidity of the air, one can calculate approximately the amount of respiration.

Still another method involves the measurement of the increasing resistance to an electric current through a standard solution of baryta water ($Ba(OH)_2$ solution) while the respiratory CO_2 is drawn through the base. As the $Ba(OH)_2$ is neutralized by the CO_2, with precipitation of barium carbonate, there is less and less electrolyte left in solution. From the increase in resistance, measured on a Wheatstone bridge, the amount of respiratory CO_2 can be calculated.[1]

2. WASTE PRODUCTS AND ASH

Wastes not useless. — In the course of the many and varied chemical changes which take place in plants, there arise, especially in consequence of the destructive metabolism, a great number of compounds which are not usable for the building of new parts, and are not again drawn into the metabolism. Some of these are nevertheless of considerable service to the plant, and in varied ways; as, for example, in protecting it from predatory animals by disagreeable tastes or odors, in covering wounds by gummy or resinous exudations, in attracting by color or odor insects which effect pollination, etc. In spite of the usefulness of some of them, these substances are often called *waste* products, and this word may well be retained instead of the more technical term, *aplastic* products, which has been applied to them. For in every household there are like products, properly "waste," so far as the direct economy is concerned, some of which may nevertheless be collaterally serviceable.

Number. — Of the reactions by which these waste products are produced, not much is known, and they need not be considered at all here. The number of the products is very great, and it is possible to name only a few of the more important groups and examples of them. An impression of their number may be gained from the fact that in a recent work on plant chemistry more than 4000 are mentioned, and the book does not pretend to enumerate all known substances. Thus there are over 200 known alkaloids, and a single firm lists some 200 essential oils of commercial value. Yet the knowledge of the chemistry of plants is very incomplete and lags far behind that of animals.

No true excretion. — Almost all of the wastes accumulate in the tissues, for actual excretion by plants is very imperfect. Except for those which are got rid of in the fragments of bark, roots, twigs, and leaves that are shed, and the relatively minute quantities that are

[1] Harvey, R. B., and Regeimbal, L. O. A conductivity cell for continuous measurements of respiration. *Plant Physiol.* 1: 205–206. 1926.

secreted by surface glands, or diffuse out into the water from roots and other immersed parts, there is no provision for doing more than storing these substances in some out-of-the-way place. In no case is there any arrangement for continuous riddance, such as is found in the excretory organs of animals. It is also particularly noteworthy that among the wastes there are few or none except the alkaloids that contain nitrogen. Even these are not necessary products of metabolism, for the very plants that produce alkaloids most abundantly may be so grown, and healthily, as not to contain any.

Gaseous wastes. — Among gaseous wastes, the most important, CO_2 and O_2, have already been mentioned; and the water resulting from respiration, while not produced as a gas, leaves the body mostly in this form. In a few plants, notably in the stinking goosefoot, cotton, and flowers of hawthorns, a very disagreeable odor makes known the escape of a gas, trimethylamin; but this is formed only in trifling amounts. In cotton, this gas is believed to attract the moth of the cotton boll-worm.

Essential oils. — Most of the odors of plants, fragrant or not, are due to the essential (volatile) oils, which are distinguishable from true oils, to which they are not at all allied chemically, by leaving only a transient spot on paper. They are especially abundant in the foliage and flowers, though there is no part but may be the seat of their production or storage. They are the more volatile constituents of complex mixtures, secreted by glands of various forms (see p. 82), whose solid residues, after the " oils " have been driven off, are resins (see below). These secretions may escape at once upon the surface, or they may be stored in intercellular receptacles and released only by crushing. In the flower leaves they are curiously distributed, being formed in the epidermis of both petals and sepals, or only in one, or only in the cells of one face, or only in lines or patches of cells. From such parts, even when in very small amounts, they may be distilled, and when more abundant they may be expressed and purified. Some are medicinal, and some are commercially valuable as perfumes for soaps, ointments, and other toilet articles. Chemically they are quite diverse; many of their constituents belong to the class of compounds known as *terpenes*. Other essential oils are aldehydes, acids, ketones, phenols, or esters. Such essential oils as turpentine, camphor, clove oil, thymol, and menthol are much used commercially.

Gums and resins. — Gums and resins occur in great variety, and often in mixtures called gum-resins and balsams. These terms are

rather loosely used, and do not designate definite chemical groups. The true gums are in large part carbohydrates, arabinose being especially abundant ($C_5H_{10}O_5$), and arise from the transformation of the cell wall and growing tissues in woody plants. They swell readily in water. Gum arabic and gum tragacanth are well known commercially, and the gum of cherry and peach trees is familiar. Resins are yellowish solids usually derivatives of essential oils, that occur dissolved in essential oils. Thus, turpentine consists of colophony or resin dissolved in "oil of turpentine," itself a mixture of several terpenes. "Canada balsam," as used for mounting sections, consists of a resin solidified by driving off the volatile oil and redissolved in a more volatile solvent. The gum-resins or balsams are variable mixtures of gums and resins, with many other accidental constituents. The best known are asafetida, galbanum, myrrh, and frankincense, the former as distinguished for its disagreeable odor as are the last three, the chief components of incense from time immemorial, for their fragrant smoke. They exude from wounds in various oriental shrubs and solidify in drops and irregular masses.

Organic acids. — The organic acids are also numerous, but four predominate. These four, oxalic, malic, tartaric, and citric acids, are all very widely distributed and are not infrequently associated. *Oxalic acid* (COOH · COOH) is not certainly known to occur in the free state, but is abundant in salts of calcium, potassium-hydrogen, and magnesium. Calcium oxalate is found in every large group of plants except bryophytes. It crystallizes in long slender needles (raphides) or as "crystal sand," with two molecules of water; or it forms large single crystals or crystal aggregates, of octahedral form, when it combines with six molecules of water. Magnesium oxalate forms spherites. *Malic acid* (COOH · CH_2 · CHOH · COOH), which is almost as widely distributed as oxalic, occurs in cacti, and in the juice of many unripe fruits, especially the apple, pear, cherry, etc., either free or in salts of calcium and potassium. *Tartaric acid* (COOH · CHOH · CHOH · COOH) is closely allied to malic acid. It is found abundantly in the juice of grapes as potassium-hydrogen tartrate. *Citric acid*

$$\left\{\begin{array}{l} \quad CH_2 \cdot COOH \\ OH \cdot C \cdot COOH \\ \quad CH_2 \cdot COOH \end{array}\right\}$$

occurs in the juice of many plants, being espe-

cially abundant in the fruits of the citrus family (lemon, lime, orange, etc.). These organic acids are all products of the incomplete oxidation of sugars.

Tannins. — The tannins are numerous and widely distributed, occurring especially in bark, wood, leaves, fruits, and galls. They are bitter and astringent substances, which form insoluble compounds with proteins and gelatine, and so are used for converting hides into leather. Tea leaves contain 14–16 per cent or more (dry weight), various barks up to 40 per cent, and galls up to 60 per cent. Some substances included in the loose term *tannins* are glucosides, and such as can be made to yield glucose by digestion may be considered as plastic substances rather than wastes. The principal tannin is made up of five molecules of digallic acid attached to one molecule of glucose.

Alkaloids. — The alkaloids are numerous, and very important medicinally, as they are dangerous poisons or useful local stimulants, according to circumstances. A few, such as *caffein* from tea and coffee, *theobromin* from the seeds of cacao (" cocoa "), and the deadly *muscarin* from the poisonous mushroom (*Amanita muscaria*), are not related to the alkaloids proper, which are for the most part derivatives of pyridin and chinolin. The true alkaloids are found in fungi and various seed plants, but are most common in certain families of dicotyls. For example, in the Papaveraceae, the oriental poppy alone yields more than twenty alkaloids, of which *morphine*, *narcotine*, and *codeine* are best known; in the Solanaceae, tobacco contains *nicotine* and others, and most of the other genera yield *atropine* and a number allied to it; a great number of the Apocynaceae have alkaloids in their latex, at least twenty different ones being known; in the Rubiaceae, the cinchonas and their allies produce more than thirty alkaloids, of which *quinine* and *cinchonine* are widely known; in the Loganiaceae, seeds of *Strychnos nux-vomica* yield *strychnine* and *brucine*, while another species yields several " *curare* " alkaloids; and in the Erythroxylaceae, coca yields among others *cocaine*, at once highly useful as a local anaesthetic and utterly destructive to body and mind when used habitually. The alkaloids are related to the amino-acids, and seem often to be produced by decarboxylization of the amino-acids.

Coloring matters of flowers, fruits, barks, seeds, etc., are too numerous and varied to be discussed here. They are mainly anthocyanins and flavones.

Ash. — Mineral salts are present, sometimes amorphous, incrusting or incorporated in the cell walls, as is the case with silica; sometimes crystallized, as is the case with calcium oxalate. The ash of plants consists of the total mineral matter left as oxides when completely burned. Analysis shows that the amount and content of the ash varies much in the same plant in different situations, thus indicating that in part (and doubtless in large part) these materials are determined not by the " needs " of the plant but by the solutions which have opportunity to wander into it. Cultures under special conditions have shown that plants may be deprived of many of the chemical elements ordinarily found, and no evil effects follow; but the absence of others has obvious ill effects. Thus silica is an abundant material in the cell walls of the epidermis of most cereals; yet corn has been cultivated through four generations with practically no silica.

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CHAPTER V. — GROWTH AND MOVEMENT

1. GROWTH

Ideas involved. — Nothing about plants as a whole is more readily seen than that they grow, and in due course unfold new organs. However small and simple, however large and complex, growth is almost always obvious, and sometimes it becomes striking because of its rapidity or its long duration. Two ideas are involved in the term *growth* as ordinarily used, (*a*) an increase in size and (*b*) the formation of new organs. The latter is sometimes distinguished under the term *development*, and if one speaks of growth and development, the term *growth* must be limited to the enlargement of already formed cells. But the terms are nearly synonymous; though growth may be restricted for a time to cells already formed, it normally leads to the formation of new organs; and though development is possible without enlargement, it is usually accompanied by an increase in size. The production of new organic material is not essential; when the corn seedling, raised in the dark, grows into a plant many times larger, the stored organic material has been merely rearranged, with the addition of water, and when the surplus food has been fully used for growth, there is actually a smaller total of dry matter than when growth began (see p. 192). Additional organic matter can be produced only when the conditions for photosynthesis are fulfilled.

Few plants have so definite a cycle of development as most animals. In some cases leaves produced in the juvenile period differ from those of later stages.[1] Again, leaves developed at certain periods are so different in form and texture as to be really different organs, as in the case of bud scales, floral parts, etc. But these periods of flowering or seed formation or other reproductive process are determined largely by external conditions, and little or not at all by the fact that the plant has reached a certain stage of maturity, though of course the formation of the special organs, as of all others, is conditioned by the supply of constructive

[1] These juvenile forms, however, may appear later under suitable conditions. See *Ecology*, chap. ii.

material. Plants, therefore, do not in general have a definite stage of maturity, and a corresponding form. They do have, however, periods characterized by growth, including the formation of new organs and their development. These periods occur once, being limited to a single season or less, as in the case of annuals; or twice, as in biennials; or they are repeated, season after season, as in perennials. This periodicity is less marked in equable tropical climates, but is rarely, if ever, entirely absent.

Phases. — If the history of any limited portion of a plant be followed (and the more limited the better, even to a single cell), it can be observed to pass through a development in which may be recognized three phases. The first phase may be called the formative phase; the second, the phase of enlargement; and the third, the phase of maturation. These phases are characterized clearly enough by certain peculiarities of structure and behavior, but they are not sharply delimited. On the contrary, the first passes by imperceptible gradations into the second, and the second into the third; then growth finally ceases, unless some unusual stimulus brings the cells again into an active state.

Formative phase. — The formative phase is the earliest. Every plant begins its existence as a single cell, and even when this one has increased to many, they usually remain practically alike. The embryo in seed plants, at the time when it resumes its interrupted growth, usually consists of cells all in the formative stage. They are characterized by a relatively large nucleus, abundant cytoplasm with only minute vacuoles, and thin walls. In this phase the frequent division of the cells is a feature, and in consequence of the more rapid production of new cells by division at certain points, the primordia of new organs appear (fig. 51). Some of the simpler plants never get beyond this phase, except as to their reproductive organs. Even in the larger plants, some of the cells permanently retain these characters, and so constitute formative centers or growing points; but far the greater number pass gradually into the

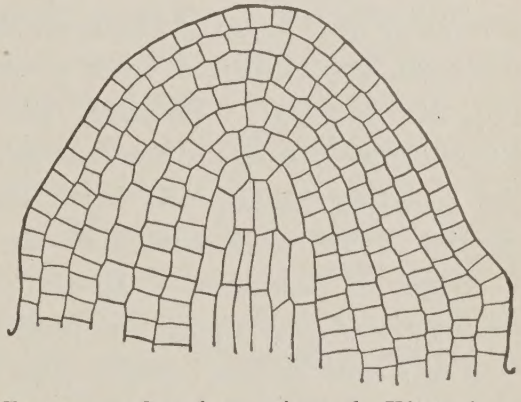


FIG. 51. — Growing point of *Hippuris*. — After DE BARY.

second phase and the third, assuming quite a different aspect and behavior. In particular, the power of division is given up.

Primary meristem. — The formative regions in thallophytes are often rather indefinite, with a tendency in the higher forms to be restricted to the apex of the body. In the bryophytes they are found only at the apex, while in the vascular plants they persist commonly at both apex and base, *i.e.* at the tip of each axis and of each root. Here the active division of the formative cells and the differentiation of their progeny adds to the length of the body at one or both ends. There may be a single cell acting as the source of all, as in ferns, or a group of initials, as in seed plants (fig. 51). The repeated division of these initials and their progeny being the important feature, the formative tissue is designated as *meristem*, and because this meristem persists from the earliest stage in the life history, it is the *primary* meristem.

Secondary meristem. — Regularly in certain regions and accidentally in others, tissues that have passed beyond the formative phase regain the power of division and exercise it for a longer or shorter time. Thus, in all plants whose xylem and phloem bundles show secondary thickening, a layer of cells between the two becomes a *secondary meristem* (cambium), and these initials may produce new cells on either face or both, which are gradually transformed into elements like their neighbors, while the initials continue to divide through the season, or function year after year. Again, a certain zone of the cortex or even the epidermis itself may resume active division, becoming a secondary meristem called the *phellogen*, whose offspring, the suberized *periderm*, constitutes a layer of cork protecting the surface (see fig. 539, *Morphology*). Wounds, the presence of a parasite, or other stimuli may call again into active division almost any live cells, and the resulting tissues will cover the wound with a *callus*, or produce the deformity characteristic of the particular injury or parasite.

Origin of branches. — In the primary meristem of the stem the primordia of new organs are produced at the surface, the first indication of a new lateral branch, whether a shoot or a leaf, being a slight elevation of the surface, due to more rapid growth of cells at that point. This mode of origin is known as *exogenous* (fig. 51) and is characteristic of branches of the shoot axis. In the root, on the contrary, the first appearance of a lateral branch is not at the surface, nor in the primary meristem, but in the pericycle (fig. 52), which lies just within the endodermis, and forms the outermost part of the stele.

The pericycle retains the capacity to become meristematic and produce new parts, even after its cells have given over for a time active division and growth. The new branch must break through the cortex, since it is *endogenous* in origin; and this is characteristic of the root axis. Adventitious growing points, giving rise to new shoots, may appear in this endogenous fashion upon roots, and likewise on old shoots or leaves. They commonly owe their origin to some external stimulus (see p. 238). Many of the growing points that are formed regularly (exogenously) on the shoot do not develop, for one reason or another. They may then be overgrown completely in woody plants, and so lie dormant for years, to be called into activity when some accident has checked the growth of others, formerly more favorably situated. Not every shoot, then, that appears to come from the interior is really endogenous in origin.

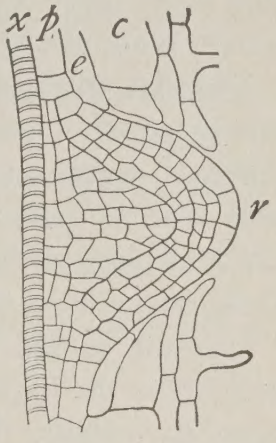


FIG. 52. — Endogenous origin of a lateral root (*r*) of ice plant (*Mesembryanthemum crystallinum*): *c*, primary cortex, and *e*, endodermis, ruptured by young root; *p*, pericycle, from which it arises; *x*, primary xylem element. — After VAN TIEGHEM and DOULIOT.

Phase of enlargement. — As cells newly formed in the meristem grow older, they enter gradually upon the second phase of development. This is characterized by enlargement, oftentimes so great and so rapid as to be very remarkable. In this period the volume of the cell not infrequently increases a thousandfold or more, though ordinarily much less. Of course this involves rapid growth of the cell wall in area, and if the cytoplasm were relatively as abundant as in the earliest stage, it would require the formation of a large mass of costly material. But while the cytoplasm does actually increase considerably, much the greater part of the cell is occupied by the water which enters it. Hence an indispensable condition for growth is an adequate supply of water; and the dwarfing which results from a deficiency of water is partly a direct consequence of the non-distension of the cells in this stage. The water enters the protoplasm, doubtless as a result of the formation of substances having a high osmotic pressure. It enlarges the minute vacuoles everywhere through the cytoplasm, until some become so distended as to merge, forming fewer but larger ones. This process continues until in the center a few large vacuoles, or often only one, occupy the greater part of the space, while the major portion of the cytoplasm lies next the

cell wall as a relatively thin layer, containing the nucleus, plastids, and other inclusions (see diagram, fig. 1). It will be apparent that since this many-fold enlargement is attained so largely at the expense of water, plant growth is relatively economical.

Unequal enlargement. — The young cell has its three dimensions nearly equal. Enlargement takes place in all dimensions, but to different degrees, according to circumstances. Thus, cells which are part of an elongated organ like a stem, are likely to grow much more in the longitudinal diameter than the transverse. The real reason for these inequalities of growth is obscure. To say that they are due to "inherent causes" or are determined by "heredity" in no wise enlightens the inquirer. In a few cases they are referable to definite agencies. Thus, the cells near the upper surface of a leaf are influenced, mainly by light, to grow longer in the axis at right angles to the surface than in the other two.[1] The sum total of growth in the individual cells determines in large measure the final form of the organ in which they lie. In most cases the causes which determine the general course of growth can be analyzed at present as little as those which determine the form of the single cell; but the effect of external agents is often detected, and in many cases it is dominant (see section 2, p. 214).

Grand period. — Enlargement proceeds at an unequal pace, even though the external conditions which affect the rate are kept uniform. In the earlier portion of the period it is slow, then it becomes more and more rapid until it attains a maximum, when it quickly falls off and gradually comes to an end. If the progress is graphically represented by plotting the increment from day to day, a curve is obtained of which figure 53 is an example. This is the history, indeed, of the growth in length of a short portion of a stem, which is made up of a multitude of cells in the phase of enlargement. In a similar way the growth in volume of a fruit, such as an apple or a pumpkin, might be described. The total period of enlargement is named the *grand period* of growth, to distinguish it from periodic variations in the rate within the grand period, some of which are due to periodically acting external agents, such as light and heat (daily period, see p. 225), and others to causes unknown and hence called "spontaneous" variations.

The same features of the course of growth may be seen when the increment of successive small portions of an axis is recorded. Thus if a root is marked into millimeter spaces, or a stem into longer spaces and the increment of each

[1] Transpiration may be another factor; the precise relation of the two is uncertain.

is recorded for a number of hours, it will appear that certain spaces are growing more rapidly than others, respectively more or less distant from the tip, *i.e.* older or younger.

The increment in twenty-four hours of each of ten 1 mm. spaces of a root of *Vicia* is here shown:

I	II	III	IV	V	VI	VII	VIII	IX	X
1.5	5.8	8.2	3.5	1.6	1.3	0.5	0.3	0.2	0.1

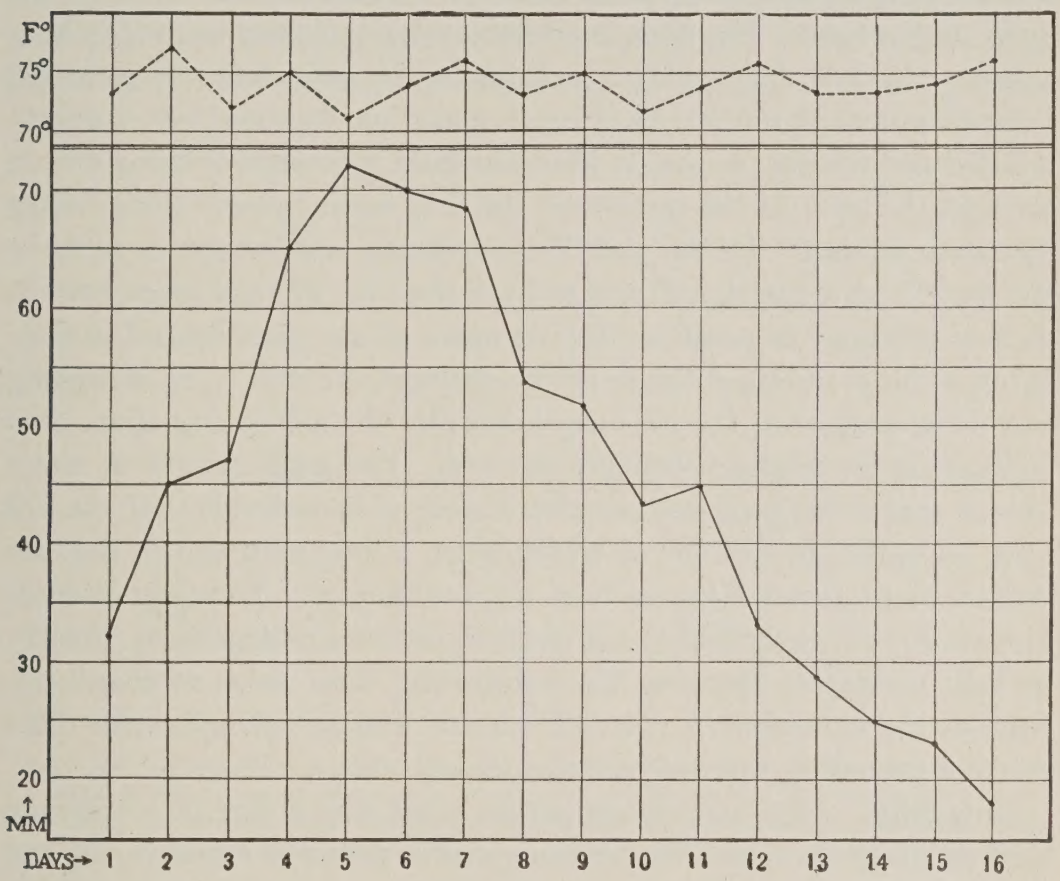


FIG. 53. — Grand curve of growth (solid line): the first day of the observation was evidently after fairly rapid growth had begun; it attained a maximum on the fifth day, with an increment of 72 mm.; thence the rate falls off rapidly, and on the sixteenth day is only 18 mm.; growth rate magnified 10 times. The temperature curve (broken line) for the same days runs between 71 and 77° F. — From data by SPOEHR.

Similarly the increase in forty hours of twelve 3.5 mm. spaces of a stem of *Phaseolus:*

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
2	2.5	4.5	6.5	5.5	3.0	1.8	1.0	1.0	0.5	0.5	0.5

Inspection of these records shows that the two younger millimeters of the root and the seven older are growing less rapidly than the third; in the stem the fourteenth to the seventeenth millimeters (space IV) are growing most rapidly, and beyond this the older a division is the more slowly it grows.

Growing regions. — Comparison of the total length of root and stem still growing appreciably shows a striking difference. About 1 cm. of the root and more than 4 cm. of the stem is shown to be growing by the record above. In general the total elongating portion of a root scarcely exceeds this; but in many stems 10–20 cm. are found elongating, and in twining plants 40–60 or even 80 cm. may be growing. The growth of aërial stems is not hindered by the medium. When they grow underground, the apex is protected by a cluster of overarching scales. Growth of such stems is seldom rapid, but when it is, as in the extensive running rootstocks of couch grass, the terminal bud is sharp-pointed and smooth, so that it offers the least resistance to being driven through the soil; at the same time the firm scales protect the primary meristem behind. In the root it is obviously advantageous to have the growth zone restricted, and to have the zone of most rapid growth as near the apex as possible; for, so much as any part behind it elongates, so far is the tip actually driven through the soil. The sloughing and slimy surface of the root cap lubricates the advancing apex, thus facilitating its passage through the soil. For good growth of roots (which makes for good growth above also), it is desirable that the soil have an optimum content of water, since it has been shown that its resistance to penetration is then at a minimum. Drought, indeed, hinders root growth doubly; it not only retards enlargement directly by lack of water, but also, by compacting most soils, mechanically opposes the extension of the root system, and so intensifies the difficulty of procuring the necessary water.

Nutations. — The rate of elongation is not only different in different sections *along* the axis; it is also unequal in different segments *around* the axis. This is especially marked in bilateral organs, such as leaves, and varies from one face to another at different periods of development. Thus, most leaves when young grow more rapidly on the back (later the under surface), so that they are appressed to the stem; or they arch over its apex when they outgrow it, as they commonly do, forming a " bud " there. Later, growth becomes more rapid on the inner face (at maturity the upper surface) and the bud opens. Local differences in rate lead to the folding and rolling so characteristic of young leaves in the bud. In radially symmetrical organs, such as stems, inequality of growth on different radii leads to bending, so that the tip is not erect but more or less declined. As the most rapid growth shifts to different segments around the axis, the tip nods successively to all points of the compass,

and so describes a very irregular ellipse or circle, or, considering also its upward growth, a very irregular ascending spiral. Plotting successive observations on a plane shows tracings like figure 54. The nodding of leaves or stems or roots on account of unequal growth is called *nutation*. The inequalities in the rate of growth may be due to unknown causes, assumed to be internal, when the corresponding nutation is called spontaneous or autonomic; or they may be due to external causes (stimuli), when the nutations are said to be induced. The latter will be particularly discussed later (see section 4, p. 245, and section 7, p. 262).

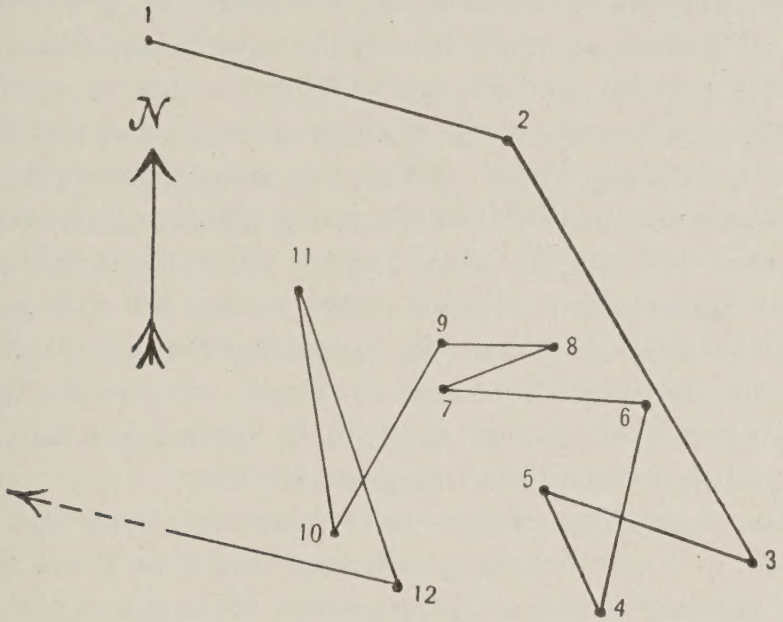


FIG. 54. — Nutations of a young sunflower plant: *1* position at 9 A.M., *2* 9:15, *3* 9:30, *4* 9:45, *5* 10:00, *6* 10:15, *7* 10:30, *8* 11:00, *9* 11:30, *10* 12 M., *11* 1:00 P.M., *12* 2:00; from point *12* the plant made a deep nod to the west till 4 P.M., then again eastward till 5:00, again westward till 6:00, and finally to original meridian at 9:00 P.M. — From data by LAND.

Rapidity. — The absolute rate of growth in the period of enlargement is, of course, extremely different in different plants and under different conditions. A few cases may give an idea of the upper limits. The filaments of wheat stamens at the time of blooming grow for a brief time at the rate of 1.8 mm. per minute, which is about the rate at which the minute hand of a man's watch travels. If such a rate continued for 24 hours, they would become 2.5 m. long. The leaf sheath of the banana grows at the rate of 1.1 mm. and that of bamboo 0.6 mm. per minute. When the century-plant blooms (as it does in 10–25 years), a shaft about 15 mm. in diameter rises to a height of 6–8 m. at the rate of about 15 cm. per day.

Growth rate. — During recent years, much attention has been given to the growth rate of organisms, and attempts have been made to express the rate of growth in mathematical terms. Blackman[1] suggested that growth of plants is like compound interest, the new growth increasing the amount of growing material, just as the interest increases the working capital. Expressed mathematically as an integral equation, he suggested that the formula $W_1 = W_0\, e^{rt}$ could be used to calculate the final dry weight of the plant. In this formula, W_1 represents the total growth or dry weight, W_0 the original dry weight of the seed or seedling under observation, r is the rate of increase, t the duration of growth, and e the base of the natural logarithms.

This idea assumes that the dry weight of a seed or seedling plant can be used as a measure of the growing material, and that the rate of growth is a constant thing. These two assumptions are not valid. There is much dead material in any living plant, and the growth rate usually varies with age, so that we cannot admit the correctness of the compound interest idea. Nevertheless, during the first part of the growth period there is an increasing speed of growth which reminds one of the compound interest increase of money. But in the last half of the growth period, the growth is gradually declining to zero rate, and of course, this is not at all like compound interest.

The rate of growth increase may be used as a sort of "efficiency index," and it would be a very valuable thing if we could only find a valid and accurate criterion of the relative efficiency of plants, to use in making selections of more efficient productive strains. Such an economy coefficient should, however, embrace many other desirable qualities besides growth rate, such as shipping quality, flavor, storage quality, resistance toward unfavorable circumstances, etc.

Another theory of growth, which has attracted much attention, is the autocatalyst theory, proposed by Robertson.[2] This theory is based on the observation that a curve of the total growth with time resembles the time rate curve of a monomolecular autocatalytic chemical reaction. The mathematical formula used to express the total growth at any given instant is: $\text{Log}\,\frac{x}{A-x} = K(t - t_1)$ in which x is the dry weight produced in time t; A is the total growth, or final dry

[1] Blackman, V. H. The compound interest law of plant growth. *Ann. Bot.* **33** : 353–360. 1918.

[2] Robertson, T. B. *Chemical Basis of Growth and Senescence.* Lippincott. 1923.

weight produced during a single growth cycle; and K is a constant which must be calculated from the data of observation. In plain English, this formula means that the logarithm of the ratio of the growth already made to that still to be made, is directly proportional to the time separating the moment of observation from the moment when the growth of that cycle is just half completed.

The growth curve, plotted in this fashion, is a sigmoid, or S-shaped curve. The first half of the curve, while growth is increasing in rate, is called the autokinetic phase; and the latter half, while growth is decreasing in rate, is called the autostatic phase of growth.

Robertson believed that growth rates are controlled by an autocatalyst, an enzyme, or growth-promoting substance like Wildier's bios,[1] which is thought to be made in the nucleus of the cell. At the time of cell division, when the nuclear membrane breaks down, this growth promoting catalyst is supposed to diffuse into the cytoplasm of the cell, and stimulate more rapid growth. But as time goes, an overaccumulation of the enzyme finally brings about cessation of growth.

While Reed [2] and others have obtained about the same kind of curves of growth in plants that Robertson did in animals, the whole theory is very unsatisfying because it depends upon a hypothetical enzyme which is not known to exist universally, and because it makes no use of other obvious facts of plant nutrition which enable one to construct a more tangible theory of the growth rate of plants.

That plants make their own enzymes cannot be denied; and that these enzymes play a part in growth may also be granted; in this sense, one can think of the growth processes as being autocatalyzed. But this is quite different from Robertson's idea of a single catalyst that controls the whole growth rate of the organism. Bakhuyzen [3] has recently pointed out the inadequacy of the Robertson theory, and shows that any formula that attempts to depict the growth rate mathematically must be made as complex as the factors which affect growth.

The sigmoid curves of plant growth are more sensibly explained by the evident nutrient conditions within the plant, and the correlations

[1] Wildiers, E. Nouvelle substance indispensable au développement de la levûre. *La Cellule* **18** : 313–331. 1901.

[2] Reed, H. S. The nature of the growth rate. *Jour. Gen. Physiol.* **2** : 545–561. 1920. Slow and rapid growth. *Amer. Jour. Bot.* **7** : 327–332. 1920.

[3] Bakhuyzen, H. L. Van de Sande. Growth and growth formulas in plants. *Science* **64** : 653–654. 1926.

that exist between the vegetative and reproductive functions of the organism. During early life the embryo depends for its growth upon the food stored in cotyledons or endosperm, which is prepared by digestion at an increasing rate as the seed germinates and the shoot begins to unfold. By the time the stored foods are exhausted, the leaves are present in such area and abundance as to produce food by photosynthesis in quantities greater than the digestion of seed reserves provided. So the growth rate continues to increase as the manufacturing machinery enlarges. This represents the autokinetic phase of the growth cycle. Finally, however, the plant approaches sexual maturity, and the nutritive supplies formerly used for vegetative growth begin to be used for reproductive functions, the building of flowers, fruit, and seeds. With the onset of flowering, vegetative growth is slowing down, and the autostatic phase is running its course; growth ultimately ceases except that the fruits and seeds continue to grow until fully formed and ready for ripening. (See fig. 55.)

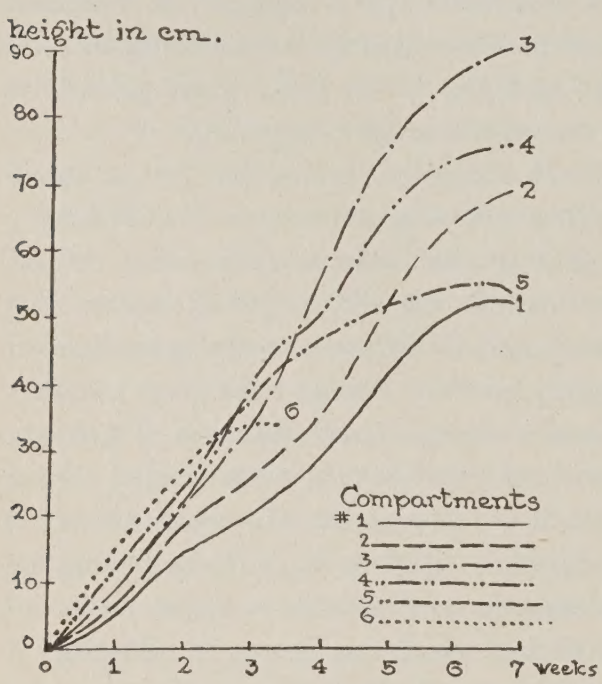


FIG. 55. — Growth curves of Ito San soy beans. Plants started to flower at end of 6 weeks. — After POPP.

From these natural changes related to nutrition, we get a sigmoid growth curve, without resort to hypothetical growth catalysts. While the studies of Murneek[1] and Popp[2] on growth correlations do not necessarily disprove the Robertson hypothesis, they offer an attractive substitute, based upon more tangible factors.

The fact that mathematical formulas can be used to calculate approximately the growth curves of plants and animals merely shows

[1] Murneek, A. E. Correlation between vegetative and reproductive functions in the tomato. *Plant Physiol.* **1** : 3–56. 1926.

[2] Popp, H. W. Effect of light intensity on growth of soy beans and its relation to the autocatalyst theory of growth. *Bot. Gaz.* **82** : 306–319. 1926.

that growth processes proceed with order and regularity under favorable conditions. The actual rate of growth is a matter partly of heredity, and is partly determined by a very complex set of environmental conditions.

Phase of maturation. — The phase of maturation is the final phase of growth. This phase is entered upon only when enlargement has practically ceased; therefore its progress is not measurable, though it is quite as important as the preceding. During this phase the cells attain their mature form and character. In all cases the thickening of the cell wall is obvious, though often slight; but sometimes it proceeds to such an extreme as to be the most notable change. The thickening is never uniform, and sometimes thin and thicker spots in patterns produce an effect of sculpturing that is characteristic, as in the tracheae and tracheids (figs. 25, 26). Conversely the resorption of certain parts of the wall may occur, as the end partitions of sieve tubes and of the components of tracheae and the thin portions of the wall in the scalariform tracheids of ferns. In case great thickening occurs, the death of the protoplast is likely to follow, and this is regularly the case in tracheary tissue. When that occurs, further modification of the wall is possible only by the agency of adjacent live cells, by chemical reaction in the wall substances, or by mere impregnation with solutes which may be precipitated or absorbed. So proceed such changes as the coloring and other alterations which mark the heart wood of trees.

Tension of tissues. — When growth is finally at an end in any region, it is found that the various tissues have not grown equally. Hence there exist strains or tensions; one region is compressed, another is stretched. These inequalities tend to adjust themselves if the regions are parted artificially, as when the pith, the bark, and the wood are separated from one another. Similarly, tensions due to unequal turgor exist (see p. 27). All these strains acting in different directions within the structure tend to increase its rigidity, just as do like strains in a latticed girder or a bridge truss.

Conditions. — The conditions for growth are first of all an adequate supply of water, for unless turgor of a meristem region is maintained, division of the cells is impossible, and unless an adequate amount of water be present, enlargement of formed cells is limited. Secondly, there must be a sufficient supply of constructive materials; for though water plays an extraordinary part in enlargement, there is needed much food for making new cytoplasm as new cells arise by division and en-

large. Nuclear material, cell-wall stuff, and much besides must be steadily constructed by the protoplasts, and the growing region is therefore the seat of intense chemical activity. Thirdly, oxygen is necessary, probably to permit the metabolism in general, and especially the respiratory changes, to proceed properly. For though growth has been observed in the absence of oxygen, it is quite limited, and, having been detected only by measurement, was probably due solely to the distention by water. Cell division also is checked by lack of O_2. Lastly, growth, like all other phenomena, goes on only within certain limits of temperature, other conditions being suitable. The optimum (different for different plants and for the same plant under different conditions) usually lies between 25° and 32° C., and the extremes are near 0° and 42° C. Any one of the conditions named may likewise vary within rather wide limits, and any one being unfavorable may retard or stop growth. Yet when all the conditions are favorable, periodic variations still mark the rate of growth, indicating clearly that there are unknown factors that operate with or against the known factors to affect it. The existence of such unknown influences is further shown by the fact that growth ceases, sooner or later, in individual cells, and often in the whole plant, in spite of all efforts to supply appropriate conditions.

External agents. — A study of growth shows that external agents produce obvious effects. They do, indeed, affect every function, and much investigation is still necessary before the full extent of their influence is known. But growth is at once so fundamental and so easy to observe, that it affords the best means for showing how extraordinary a part external agents play in determining the form and behavior of plants.

A few of the major factors that influence plant growth may be considered briefly here, including mineral nutrition, toxic inorganic compounds, organic compounds, temperature, light, oxygen supply, carbon dioxide supply, electroculture, and the influence of organic and other stimulants.

2. EXTERNAL AGENTS

The most general fashion in which various external agents affect growth appears in the way they control the form of the body through local alterations in the development of various parts. The varied and diffuse stimuli are termed *formative* or *morphogenic*. The reactions to them are extremely difficult to study because both stimuli and reactions

are so general, and particularly because experimental alteration of one factor is almost certain to alter others to an unsuspected or an uncontrollable extent; wherefore the analysis of the factors operating is rendered very uncertian.

Chemical agents. — Chemical stimuli are extremely important in determining the form of plants. The presence or absence of particular substances in the cells, whether foods or wastes, doubtless exerts a profound influence. But the precise influence of the different compounds cannot be determined satisfactorily, because the chemical processes within the plant are so imperfectly known. It is in this region that the rôle of the so-called necessary elements of the ash, calcium, magnesium, potassium, and iron are to be sought, in all probability. How far the xerophytic structure of plants is to be ascribed to the lack of water is not certain. The deficiency of available water is in itself a chemical stimulus by determining the direction of reversible chemical reactions, and it may make possible the stimulating action of other substances within the plant, which, but for their increased concentration, would not act so. Unquestionably, other causes than lack of water around the roots of a plant may call forth such structures, as is well seen in the case of bog plants. Indeed it has become customary to speak of "physiological" drought as the cause of xerophytic structure, when physical drought is obviously out of the question. This may be taken as a convenient expression for some difficulty which prevents the plant from admitting a sufficient amount of water, such as the poor development of the root system. Whatever does this will tend to dwarf or otherwise transform the aerial parts, either as the plain lack of water does, or possibly in quite different and unrecognized ways. (See further, *Ecology*, on dwarfing in bogs.)

Careful investigations have brought to light some other causes for the imperfect development of plants, which probably is due primarily to an effect on the roots. It is found that the sterility of some soils is due to the presence in these soils of organic substances, which are partly soluble, so that a watery extract of such soils, when used as a water-culture medium, acts as badly as the soil itself. Furthermore, these substances can be removed in large part by adding some finely divided material like lampblack to the liquid and then filtering it out. The filtrate may then be used without detriment to the cultures. Still further study makes it probable that these substances originate in large part from the plants which have previously grown in the soil. The necessity for the rotation of crops on any field has long been known. The reason has been assumed to lie in the exhaustion of the materials which are supposed to be necessary for the nutrition of the plants. Without denying

that there may be something in this assumption (it is nothing else at present, because the experimental evidence upon which it rests is faulty), it seems now much more likely that the chief cause is to be found in the products of root decay in the soil. It has been shown that though the mineral salts of a culture solution be maintained unchanged, the water becomes more and more unfit for use with repeated cultures of the same species, and that this impairment may be remedied by treatment with lampblack as above described, though the content of salts be not altered. Water cultures, to which have been added various organic substances that might be produced, or are known to occur in plants, have shown like injuries to the plants, and though the amount of the deleterious substances occurring in nature is too small for direct analysis, their general character may be ascertained by further experimentation in this way.

Mineral nutrients and plant growth. — The functions of the various minerals in the physiology of the plant were discussed in an earlier chapter. Something like twenty elements have been proved necessary for the proper development of plants. This includes traces of such elements as aluminum, boron, fluorine, iodine, zinc, copper, manganese, chlorine, silicon, etc., in addition to those required in large amounts. The main problems center about limiting factors, and physiological balance of nutrients in the growth medium.

Any mineral may become a limiting factor upon growth. The Liebig-Blackman [1] conception of limiting factors is that the plant yield in dry weight is dependent upon that factor which, relatively speaking, is most nearly at a minimum. But the situation is not so simple as Blackman depicted it. If two mineral nutrients are equally limiting, the addition of one of them to the soil should not lead to increased growth of the plant; but it nearly always does cause increase to add only one of a pair of limiting factors. The law of the minimum does not apply with such rigidity as we sometimes tacitly assume. Again we often find that for a limiting factor something else can be substituted. Thus when absence of light seems to be a limiting factor on the germination of seeds, and we find that we can replace light by use of nitrate solutions, or acids, or bases, or some temperature condition, in releasing germination, we see that the problem of limiting factors becomes more obscure in the presence of substitution factors.

A great deal of work has been done on physiological balance of mineral nutrients. During the five years from 1913 to 1918, the

[1] Blackman, F. F. Optima and limiting factors. *Ann. Bot.* **19**: 281–295. 1905.

fundamental researches of Tottingham,[1] Shive,[2] McCall,[3] Livingston,[4] and others appeared, leading up to the development of three-salt culture solutions containing the six ions, Ca^{++}, K^{+}, Mg^{++}, NO_3^{-}, HPO_4^{--}, and SO_4^{--}, to which iron was added as iron phosphate. Beginning in 1919, under the influence of the National Research Council, a coöperative project was outlined to determine the best physiological balance of mineral nutrients at each stage of the life history of wheat and soy beans.

The salt solutions were prepared in different proportions of ions, but with a constant total osmotic pressure of one atmosphere, and set up in triangular fashion. The best proportion of nutrient ions was determined by which culture made the best growth. Many plants, including rice, corn, buckwheat, Canada field peas, potatoes, cotton, etc., were tested by various investigators, and a best solution sought. Many difficulties were encountered and the project has failed as a coöperative enterprise. The main reasons for this are, that variability of individual plants even in pedigreed strains is so great that about 100 plants must be grown to each culture to obtain a reliable average. Since only five plants should be grown in a single good-sized culture jar, it would require 20 replications of a single nutrient solution culture to secure enough plants, or 420 cultures for a complete experiment representing one triangular set of experiments. In addition it was found that the nutrient solution must be kept flowing[5] to prevent change in ion concentration and reaction value (hydrogen ion concentration) of the solution. It was further observed that seasonal effects prevent duplication of results. A magnesium injury found in March failed to develop in plants grown in the same kind of solution in December. Locality differences would no doubt play a rôle in confusing the results also, so that coöperation at widely separated places would not yield valid results. And since the results from solution culture cannot be interpreted in the terms of soil culture, there seems to be little advan-

[1] Tottingham, W. E. A quantitative chemical and physiological study of nutrient solutions for plant cultures. *Physiol. Res.* **1**: 133–245. 1914.

[2] Shive, J. W. A study of physiological balance in nutrient media. *Physiol. Res.* **1**: 327–397. 1915.

[3] McCall, A. G. Physiological balance of nutrient solutions for plants in sand cultures. *Soil Sci.* **2**: 205–253. 1916.

[4] Livingston, B. E., and Tottingham, W. E. A new three-salt nutrient solution for plant cultures. *Amer. Jour. Bot.* **5**: 337–346. 1918.

[5] Trelease, S. F., and Livingston, B. E. Continuous renewal of nutrient solution for plants in water culture. *Science* N. S. **55**: 483–486. 1922.

tage in such studies, except for the accumulation of knowledge of plant behavior under controlled highly artificial conditions.

Some of the results obtained threw doubt upon the importance of physiological balance. Hoagland[1] believes the range of physiological balance is so broad, if the proper total supply, concentration, and variety of elements are present, as to include most soil solutions. Duggar[2] has also expressed the belief that there may be no "best" solution, but a considerable range of proportions within which the plants do about equally well, depending somewhat on other environmental conditions. Certainly in soils, the type of soil, the temperature of the soil, the moisture supply about the roots, and aëration have great significance in connection with mineral nutrition and growth.

Other methods of attacking the problem of mineral nutrition and growth are likely to yield more permanent results. It has been shown by a study of paired ions,[3] for instance, that the plant grows better when it receives K and NO_3 ions at the same moment than if they are absorbed separately. By varying the time of the application of nitrogen to the soil, it has been found possible to almost double the protein content of White Australian wheat.[4] Thus addition of nitrate when the wheat was 17 days old gave grain with about 8.5% protein. But the same application of nitrogen when the wheat was 110 days old gave a wheat with 15.2% protein.

Some of the mineral elements, if supplied during the first few weeks of life, can be dispensed with later. Magnesium, phosphorus, and sulphur are said not to be needed after the first few weeks if the early supply is adequate. But iron and calcium must be supplied throughout the life of the plant in order to insure proper growth.[5]

Toxic inorganic compounds. — In addition to the nutrient elements there are some that are indifferent as far as plant growth is concerned, and others that are probably definitely toxic, even in low concentra-

[1] Hoagland, D. R. Relation of the concentration and reaction of the nutrient medium to the growth and absorption of the plant. *Jour. Agr. Res.* **18**: 73–117. 1919.

[2] Duggar, B. M. Hydrogen ion concentration and the composition of nutrient solutions in relation to the growth of seed plants. *Ann. Missouri Bot. Gard.* **7**: 1–49. 1920.

[3] Gericke, W. F. On the physiological balance in nutrient solutions for plant cultures. *Amer. Jour. Bot.* **9**: 180–182. 1922.

[4] ———. Differences effected in the protein content of grain by applications of nitrogen made at different growing periods of the plants. *Soil. Sci.* **14**: 103–109. 1922. See also *Science* N. S. **52**: 446–447. 1922.

[5] ———. Salt requirements of wheat at different growth phases. *Bot. Gaz.* **80**: 410–425. 1925.

tions.[1] Such toxic elements may even kill the plant if the concentration is great enough. Any salt may become toxic by overdosage through the effects of too great concentration about the roots. But such elements as Cu, Zn, As, B, Hg, Ag, Au, etc., are distinctly poisonous when present in more than mere traces. This is true notwithstanding the fact that boron, copper, and zinc may be necessary in traces for successful growth.

The lethal concentration of copper salts is about 0.005 per cent to 0.006 per cent, but in the presence of calcium salts the copper toxicity is much reduced owing to the general antitoxic action of calcium. Soils reduce the toxicity of copper by adsorption effects. Some plants are highly resistant to copper. Fungi have been known to grow in a molecular solution of copper sulphate. In this case probably very little copper ever penetrates the limiting membranes of the plant. On the other hand, some of the algae are very sensitive to copper. *Spirogyra* is killed by one part of copper in fifty million of water, and *Anabaena* and *Oscillatoria* are only slightly less sensitive. On this account copper salts may be used to clean water reservoirs of algal contaminations.

Zinc is toxic if used in too large amounts, although plants require small amounts of zinc for proper development. Some soils contain zinc salts in abundance, as in the case of calamine soils; and sphalerite sometimes occurs abundantly in soils. Plants that grow on such soils contain notable quantities of zinc, but the vegetation of calamine soils is usually sparse and poor. Zinc sulphate is toxic to clover, vetch, and beet at concentrations of 1 : 25,000 to 1 : 50,000, and is even more toxic to barley and radishes. The main effect is on root growth, which is very poor in such concentrations of zinc salts. Some of the fungi, like *Aspergillus*, are said to show great stimulation by low concentrations of zinc in the growth medium. Arsenic in the form of arsenious acid, arsenious oxide, and arsenites is quite toxic, somewhat more so than arsenic acid and the arsenates. Barley shows little growth at concentrations of 1 : 10,000 to 1 : 20,000.

Boron becomes toxic if too much is used. The main salt we need to consider is borax. When desert lake deposits are used for fertilizers, borax sometimes causes trouble. Such fertilizers must run less than 0.5 per cent borax, or they cause injury. Cotton is distinctly injured

[1] Brenchley, W. E. *Inorganic Plant Poisons and Stimulants*. Cambridge Agricultural monographs. 2d ed. Macmillan Co. 1927.

if 20 pounds of borax are applied per acre. The reduction in yield is 15 to 25 per cent by such an application.[1]

Manganese may cause difficulty, if it is too concentrated. It is necessary to growth in concentrations of less than 1 : 100,000, but it becomes somewhat toxic at greater concentrations. Where manganese minerals form a large proportion of the soil, as in the red soils of Hawaii, the soils may be injured by the precipitation of iron in a form too insoluble for the plants to obtain it.

Ferrous and ferric salts are said to be toxic to plants; the former the more toxic, and certain plant disorders have been thought to be due to over-accumulation of iron in the tissues.[2] There seems to be a narrow range of iron balance in the plant, and either too much or too little iron is injurious. Aluminum has similarly been mentioned as a possible source of toxicity, and it may be too abundant in certain acid soils.

Over-abundance of hydrogen ion in the soil is also a toxic condition. The range of soil acidity is from pH3.7 to 9.7, with 4.5 to 8.5 the usual range. When the hydrogen ion concentration is too great, the protoplasm of the root hairs of plants grown in acid medium suffers coagulation which impairs the function of the hairs or kills them outright.[3] Soils must therefore be kept at an appropriate reaction value for good growth of plants. This is done by giving applications of lime to soils that show a high lime requirement.

Organic compounds and growth. — While decaying humus is necessary to a fertile soil, some of the products of decay are now known to be injurious. Soil chemists have isolated more than thirty such compounds from soils during recent years.[4] Among them may be mentioned such compounds as dihydroxystearic acid, α-crotonic acid, and various other acids, aldehydes, phenols, and alkaloids. These are probably all decay products, but if for some reason they accumulate locally, they produce an infertile soil. Such products are destroyed in the soil by bacterial action, so that accumulation is not common.

[1] Skinner, J. J., and Allison, F. E. Influence of fertilizers containing borax on the growth and fruiting of cotton. *Jour. Agr. Res.* **23** : 433–443. 1923.

[2] Hoffer, G. N., and Trost, J. F. The accumulation of iron and aluminium compounds in corn plants and its probable relations to root rots. *Jour. Amer. Soc. Agron.* **15** : 323–331. 1923.

[3] Addoms, R. M. The effect of the hydrogen ion on the protoplasm of the root hairs of wheat. *Amer. Jour. Bot.* **10** : 211–220. 1923.

[4] Skinner, J. J. Soil aldehydes. *Jour. Franklin Inst.* **186**: 547–584, 723–741. 1918. See also *Bureau of soils Bull.* 53. 1910.

The idea that crops can injure succeeding crops by excreting substances through the roots into the soil has persisted through many years of investigation, but without adequate experimental evidence. Grass is believed to be injurious to apples, for instance. The injury may be due in large measure to the competition of the grass roots with apple roots for oxygen and nitrates.

It has been claimed that *Sesamum indicum* will not mature within two feet of sorghum plants.[1] The plants die when a few centimeters tall. Such a sensitive plant should be useful in testing out the possibility of toxic excreta from living plants. In such cases as the injurious effects of sorghum on succeeding wheat crops, it seems more probable that toxic substances arising by the decay of the sorghum roots may be responsible for the injurious effects. Sewell[2] has shown that unoxidized soil extracts of sorghum soils do depress the growth of other plants.

On the other hand, growth-promoting organic compounds have been sought, and certain unknown components of bacterized peats have been called auximones,[3] or growth promoters. The experimental basis of the claim that auximones exist is faulty, for in most cases the plants tested were grown on rather poor nutrient solutions, and the auximone preparations added contained many other nutrients, so that the addition involved better nutrition all round. If, for instance, we grew plants on a solution of ammonium tartrate and glycerine, we would get very poor growth no doubt. Then if we added a drop or two of raisin juice, we would certainly get much better growth. But we cannot from such a test prove the presence of auximones and vitamins in raisin juice. We have simply bettered the general nutritive conditions of the culture medium. The nutrient medium must always be adjusted to give the maximum growth without organic additions before we attempt to prove that the organic compounds are growth-promoting substances. Vitamins may be necessary for plant growth just as they are for animal growth, but the plants obtain them by

[1] Fletcher, F. Toxic excreta of plants. *Jour. Agr. Sci.* **4** : 245–247. 1912.

[2] Sewell, M. C. Effect of *Andropogon sorghum* on succeeding crops of *Triticum sativum vulgare*. *Bot. Gaz.* **75** : 1–26. 1923.

[3] Bottomley, W. B. The effect of auximones on the growth of *Lemna minor* in nutrient solution. *Proc. Roy. Soc.* Lond. B. **39** : 483–506. 1917.

Wolfe, H. S. The auximone question. *Bot. Gaz.* **81** : 228–231. 1926.

Ashby, E. The interaction of factors in the growth of *Lemna*. *Ann. Bot.* **43** : 333–354. 1929.

natural synthesis within their own tissues possibly by the action of short radiations of sunlight upon some of the products of metabolism.

Temperature and growth. — Each species of plant has its own minimum, optimum, and maximum temperature relations. The minimum temperature for growth is usually somewhat above freezing, and the maximum in the neighborhood of 45° to 50° C., except in thermophile organisms which may be able to survive in temperatures considerably higher. The optimum temperature usually falls around 30° C. for ordinary plants.

When the temperature is below the optimum for any given set of conditions, increasing the temperature increases growth. The temperature coefficient of growth varies with conditions, but a ten-degree rise often doubles or trebles the growth rate, which agrees fairly well with Vant Hoff's temperature rule.

The formative effects of temperature are very important in plants. The plant body may be entirely different at low temperatures than at high temperatures. One of the filamentous algae, *Stigeoclonium*, changes to a unicellular form at low temperatures, for instance. The potato plant grows with a short stocky shoot at 15° to 18° C., but grows long and slender etiolated shoots at 26° to 29° C.[1] The fruiting habits of the eel grass, *Zostera marina*, is controlled by temperature;[2] and by a combination of high temperature and short day, cockleburs can be made to form blossom buds in less than two weeks from the seed.[3]

In the case of dormant plant organs, as seeds, bulbs, corms, etc., low temperatures may be used to cause rapid after-ripening and overcoming of dormancy. A temperature of about 5° C. has been found best for this purpose.

For twigs the warm bath may be used, which consists in treating the twigs with warm water for several hours. The warmth and soaking start up the life processes in treated twigs long before the untreated twigs become active. It has been claimed that the temperature conditions which prevail during germination or in early seedling stage may determine the character of growth in later life. Seedlings of

[1] Bushnell, J. W. The relation of temperature to growth and respiration in the potato plant. *Minnesota Agr. Exp. Sta. Techn. Bull.* 34. 1925.

[2] Setchell, W. A. *Zostera marina* in its relation to temperature. *Science N. S.* **56**: 575–577. 1922.

[3] Gilbert, B. E. Interrelation of relative day length and temperature. *Bot. Gaz.* **81**: 1–24. 1926.

kohlrabi treated with temperature at −2° to −8° C. were caused to bloom without forming the usual swellings on the stems. Such plants as beets and celery may be caused to blossom prematurely, without storing the usual quantities of food. Cereal grains may also be modified in their behavior by temperature. Gassner reported certain cereals as recumbent in habit if the germination temperature was too high.[1] Cold-treated seeds grew erect from the start, and formed culms much earlier. Seeds given a germination temperature of 6° to 9° C. for five days, and then two days at 25° C. formed culms in about two months, while those given the warm temperature first, followed by cold (2 days at 25° C. and 5 days at 6°–9° C.), went through the winter without culm formation.

While more data are needed on these points, it appears that the temperature of germination may exercise a physiological predetermination upon growth.

Barley shows excessive vegetative growth at high temperatures (25° C.). Walster[2] reports this particularly if a high soluble nitrogen supply is given at the same time. The leaf shows high soluble nitrogen content and low carbohydrate content, which gives a low carbohydrate : nitrogen ratio. The effect of this internal metabolic condition is excessive vegetation and poor culm formation.

If low temperature (15° C.) is used, the metabolic conditions of the leaf are reversed. The carbohydrate supply is high, and the soluble nitrogen of the leaf is low. This gives a high carbohydrate : nitrogen ratio, and the result is normal vegetation and normal culm formation.

These results are in harmony with the work of Kraus and Kraybill[3] who showed that the vegetative and reproductive functions of the tomato can be controlled by controlling the internal carbohydrate : nitrogen ratio.

The accumulation of carbohydrates in the leaves at low temperature has an effect upon the root-top ratio of the plant. High carbohydrate content, which goes with low temperature, favors root development in the cereal grains, while a high nitrogen supply is more favorable to top development. In the potato also the low tempera-

[1] Gassner, G. Beobachtungen und Versuche über den Anbau und die Entwickelung von Getreidepflanzen in subtropischen Klima. *Jahresb. für ang. Bot.* **8**: 95–163. 1910.

[2] Walster, H. L. Formative effect of high and low temperatures upon growth of barley : a chemical correlation. *Bot. Gaz.* **69**: 97–126. 1920.

[3] Kraus, E. J., and Kraybill, H. R. Vegetation and reproduction with special reference to the tomato. *Oregon Agr. Exp. Sta. Bull.* **149**. 1918.

ture is favorable to high carbohydrate content of leaves, and leads to good tuberization.

The accumulation of carbohydrates in the leaves at low temperatures more than at high temperatures is probably due to lowered respiration. The food left for growth or storage is the amount by which photosynthesis of carbohydrates exceeds the immediate use of carbohydrates in respiration, etc. Since the optimum temperature for the respiratory process is higher than for photosynthesis, the food left for storage as the temperature rises is less and less, and in the potato less and less tuberization occurs as the temperature rises. This accounts in part for the fact that cool seasons are best for potatoes, and that Maine and Idaho, with their cool summer climate, are our best potato regions.

These facts all emphasize the significance of temperature as a formative factor in plant life. But it is a superficial factor. It must exert its control through some deep-seated effects like the change in the carbohydrate : nitrogen ratio, or other similar internal metabolic changes. The changes in metabolism are no doubt to be looked upon as the real causes of the observed behavior.

Temperature also has a prominent relation to the incidence of soil-borne diseases of plants.[1] Such diseases as cabbage yellows, flax wilt, tomato wilt, tobacco root rot, seedling blight of wheat and corn, and many other diseases are severe at certain soil temperatures, and much less severe at other temperatures above and below the optimum for the disease organism.

However, the disease organism may find its entry into the host plant made easier or more difficult by the effects of temperature on the roots of the host plant. Corn is injured by seedling blight at low temperatures more than at high, while wheat is more susceptible at high temperatures. Preliminary studies have indicated that corn roots have more pectic material in the walls of the cells of the roots at abnormally low temperatures (12°–16° C.) while the walls are more cellulosic at high temperatures.[2] Wheat, on the other hand, produces pectic-walled cells at high temperatures, and cellulose walls at low. The fungus penetrates the cell walls more easily when they are pectic, and

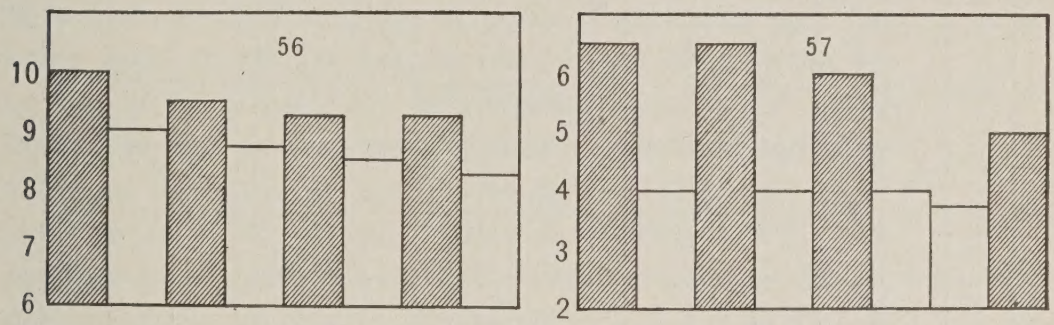
[1] Jones, L. R., Johnson, James, and Dickson, James G. Wisconsin studies upon the relation of soil temperature to plant disease. *Wisconsin Agr. Exp. Sta. Res.* Bull. **71.** 1926.

[2] Eckerson, S. H., Dickson, J. G., and Link, K. P. The nature of resistance to seedling blight of cereals. *Proc. Nat. Acad. Sci.* **9**: 434–439. 1923.

less readily when they are cellulose. These considerations help to account for the greater susceptibility of corn in a cool season and of wheat in a hot season, to the ravages of *Giberella saubinetii*.

The susceptible strains of certain grains may be due to constitutional differences of behavior in the host metabolism. Any strain of host plants that inherits a tendency to form pectic-walled cells in the root would be more susceptible to attack by organisms that find entry easier.[1]

Light and growth. — It is well known that the rate of growth rises and falls with the temperature, and since heat and light are both forms of radiant energy, it might be expected that the shorter and faster light waves would also affect the rate of growth. This proves to be true.



FIGS. 56, 57. — Graphs showing growth in millimeters in alternating period of darkness (shaded) and light: 56, sporangiophore of *Mucor mucedo*, periods 15 minutes; 57, rhizoids of *Marchantia polymorpha*, periods 20 minutes. — Based on data by STAMEROFF.

In general the effect of light is to retard growth, following a brief period of stimulation, which will be mentioned again in a later section.

This is especially noticeable in elongating organs. It is very clearly seen in the sporangiophores of *Mucor* and the rhizoids of *Marchantia*, as will appear from the graphic representation of the observations (figs. 56, 57). It comes out also in the autographic records of the growth of elongating stems when plotted so as to show the increment during the day and during the night, the temperature and other conditions, of course, being kept as constant as practicable.

Daily period. — In nature the retardation due to light is doubtless accentuated by the greater evaporation of the daytime; but it is more or less compensated by the acceleration due to the rising temperature. Contrariwise, the acceleration upon the coming of darkness and a moister air is partly offset by the retardation due to the lower tem-

[1] Dickson, J. B., and Holbert, J. R. The influence of temperature upon the metabolism and expression of disease resistance in selfed lines of corn. *Jour. Amer. Soc. Agron.* 18: 314–322. 1926.

perature of the night. Nevertheless, a periodic variation in growth in length, corresponding to the day and night, and hence called the *daily period*, can be traced, unless the fluctuations of temperature are excessive. This means that as certain conditions act antagonistically upon the rate of growth, they may be balanced or one set may overcome the other. The difference between the darkness of night and the light of day is so much greater than the usual differences of temperature and

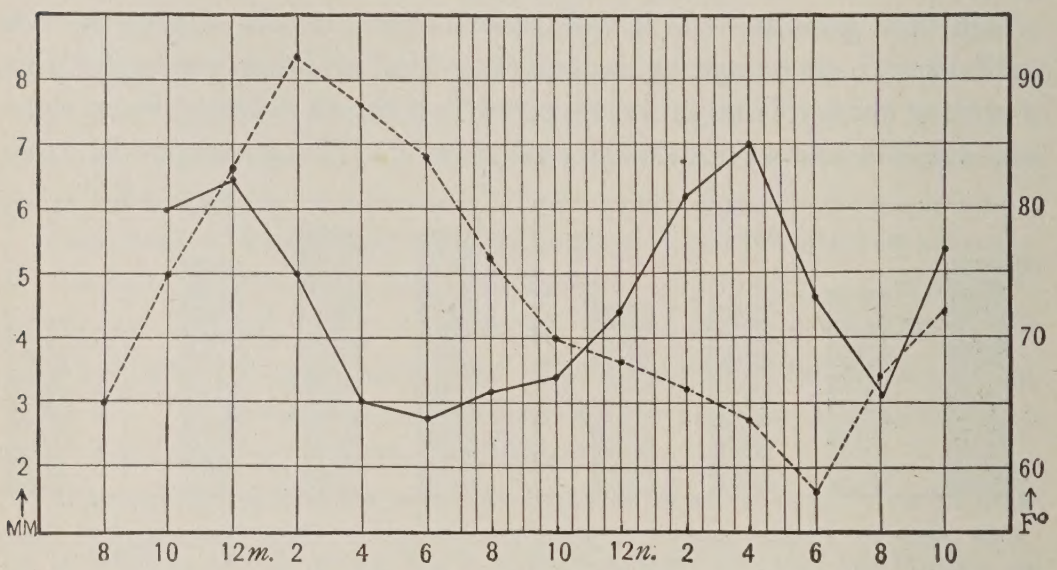


FIG. 58. — Curve of daily period (solid line) and of temperature (broken line): each vertical interval corresponds to 1 mm. increment for the growth curve and to 5° F. for the temperature curve; horizontal intervals are hours, the region of close-set lines showing the night. Note rapid growth during the first day, beginning to fall off before the temperature falls (probably a transpiration effect) and then rising in the night in spite of falling temperature (partly also a moisture effect). — From data by SPOEHR.

moisture in these hours, that the light effect is likely to be dominant (fig. 58).

Light and form. — The form of the aërial parts of most plants is profoundly influenced by light, directly or indirectly. This is shown by the striking changes that ensue (*etiolation*) when they are grown in darkness. Without starvation this is possible only with plants that have already stored a sufficient amount of surplus food. One who has observed the long pallid shoots of a potato which has sprouted in the dark will have seen the general effects. The stems tend to elongate much more than usual, though they are not necessarily more slender; the branching is at a different angle; and the leaves remain small and imperfectly developed. (The pallor from lack of chlorophyll and the presence of carotin are features already mentioned.) On the whole,

elongation is likely to be accentuated, breadth is likely to be repressed (fig. 59). Though these are the common results of the lack of light during development, they are by no means universal. Thus, there are plants whose stems do not elongate, and others whose leaves are not reduced. But if not these, other characteristics may be altered; *e.g.* reduction of the mechanical elements of the tissues is one of the less obvious effects. Scarcely a plant escapes but those that pass all their lives in darkness, and only those parts that are buried in the soil are exempt from the formative influence of light.

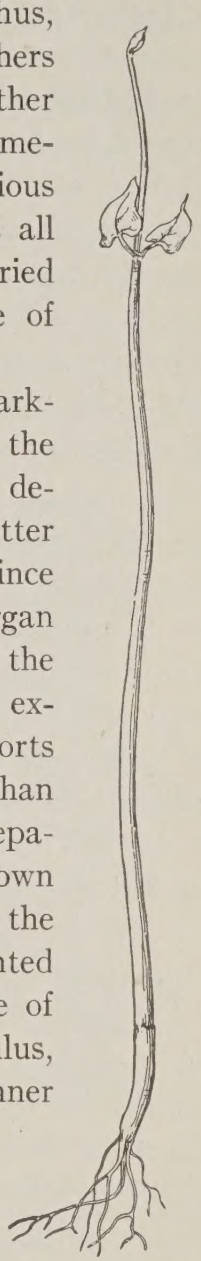


FIG. 59. — Plant of *Phaseolus* grown in darkness. — After MACDOUGAL.

Dorsiventrality. — In plant organs not grown in darkness, but of which one side is better illuminated than the other, light effects can be observed. One effect is the development of a distinctly different structure in the better lighted surface as compared with the shaded one, and since these are naturally the upper and under surfaces, an organ showing such differences is termed *dorsiventral*.[1] Thus the palisade portion of the mesophyll of leaves owes its existence chiefly to light.[2] Dorsiventrality in the liverworts is likewise due mainly to light. None shows this better than the common *Marchantia*. If a gemma which, when separated from the parent, is just alike on the two sides, be grown in a moist chamber with the lower side illuminated and the upper dark, air chambers will be developed on the lighted side and rhizoids on the dark one, exactly the reverse of the usual relation. Gravity, if it furnish any stimulus, as is probable, is clearly overcome by light. In like manner light determines the formation of the sex organs upon the under side of fern prothallia. A striking example of light effects among the seed plants is to be found in the dorsiventrality of the root-stocks of the spatter dock (*Nymphaea advena*). These great rhizomes develop at the surface of the mud at the bottom of pools, and are of the length and thickness of a man's arm. From the upper side numerous leaves arise, and from the under side

[1] Dorsiventral organs may owe the difference of their faces to other formative stimuli, *e.g.* to gravity.

[2] See footnote, p. 207.

roots. This distribution of organs is found to be determined by differences in lighting.

Light and development. — Light is of great importance at every stage of the development of the green plant from germination of the seed to full maturity, mainly because light is necessary to the manufacture of food upon which growth and development depend. There are at least four variables to deal with in light phenomena, the intensity, the quality, the duration, and the direction of the light. If we know the intensity, the quality, and the duration of the light, we have a fairly complete picture of the energy playing upon the plant. The direction from which the light reaches the plant has mainly to do with the tropic responses in which light plays a part. The intensity of the illumination may be measured by the use of pyrheliometers, or by the MacBeth illuminometer, and is usually expressed in foot-candles. Bright sunlight may reach 6000 to 8000 foot-candles.

FIG. 60. — Cosmos about 60 days old. Those receiving light for only about 6 hours are in bloom. The 15-hour plants (right) are completely vegetative. — After WEAVER.

The quality of light is expressed in terms of range of wave lengths. The visible rays of light range between 400 μ and 720 μ.

The duration of light may be continuous or intermittent. Natural light is intermittent, with the day length ranging from about 15 hours at the summer solstice to nine hours at the winter solstice. The day length has much to do with the blooming time of plants.[1] When a plant responds noticeably to the relative length of day and night, it is said to be photoperiodic. Some plants like poinsettia bloom and develop bright colors only during the short day portion of the year. Chrysanthemums and late cosmos are other examples of short-day plants. (See fig. 60).

[1] Garner, W. W., and Allard, H. A. Flowering and fruiting of plants as controlled by the length of day. *U. S. Dept. Agr. Yearbook.* 377–400. 1920. See also, *Jour. Agr. Res.* **18** : 553–606. 1920.

Similarly, we have long day plants, like soy beans, clover, and many other summer blooming varieties of flowers. Other plants blossom when the days and nights are about equal. These may be called equatorial day plants.

Some plants are not so sensitive to photoperiods, and may bloom at almost any time of year. Dandelions, for instance, have been found blossoming in every month of the year.

Germination. — Light affects the germination behavior of certain species.[1] Such plants as tobacco, mistletoe, certain grasses, mullein, carrot, etc., either require light for germination, or give better germination with light. But *Phacelia*, *Nigella*, *Datura*, *Amaranthus*, and some others refuse to germinate in light, or do much better in darkness.

In some cases the light sensitiveness of seeds is lost if the coats are removed, as is the case with *Chloris ciliata*, one of the grasses which needs light for good germination. This suggests that light may change the colloidal conditions in the seed coat which control the water and oxygen relations of the embryo. This change in the colloids of the seed coat may be associated with the presence of colloidal iron which in the presence of light may cause hydrolysis, and through this exert an influence on germination. If, for instance, seeds with a thick endosperm show only a superficial hydrolysis of the stored food in light, and a deep-seated hydrolysis near the embryo in darkness, this difference in accessibility of digested food to the embryo might determine whether the seed would germinate in darkness or in light.

Growth responses. — A growing organ or part of the plant usually shows a double response to changes in light intensity. There is a primary response of more rapid growth, followed by a secondary response in which the growth rate is retarded.[2] If we compare the growth curve of the coleoptile of *Avena* in darkness with the growth curves in light, we find that the greater the intensity of light, the more sharply the growth curve rises, but the lower the maximum point of the curve, and the earlier it falls off to zero. The total growth is found to be inversely proportional to the intensity of the light — the more intense the light, the less total growth in length.

The quality of light falling upon the plant has much to do with the

[1] Gardner, W. A. Effect of light on germination of light-sensitive seeds. *Bot. Gaz.* **71**: 249–288. 1921.

[2] Sierp, Hermann. Untersuchungen über die durch Licht und Dunkelheit hervorgerufenen Wachtumsreaktionen bei der Koleoptile von *Avena sativa* und ihr Zusammenhang mit den phototropischen Krümmungen. *Zeitschr. f. Bot.* **13**: 113–172. 1921.

kind of development that takes place. Most of the earlier experiments with colored screens failed to record the intensity of the light used, so that the results are unreliable.

The work of Schanz [1] about ten years ago indicated that plants grow taller the more the short rays are removed by screening them out. Maximum growth occurred in red light and minimum in the blue in certain plants like the cucumber, petunias, begonias, etc., but potatoes and red beets were larger and more robust in blue violet light. Epidermal anthocyanin failed to develop in lettuce when the short rays were screened out. Blossoming was hastened by removal of these short rays, and the number of flowers and fruits were increased where the short rays were removed. The germination of nettle seed was favored by removal of the short rays. But even in this work, the intensity of the light used was not recorded, and other conditions were not definitely stated, as for instance the temperature at which the greenhouses were kept. Popp [2] has recently made very careful studies of the growth of plants under different ranges of wave length, where the intensity of illumination was known. He found that the short visible rays of the blue-violet end of the spectrum are necessary to the normal growth of the plant. When all of the short rays were removed, the plants became etiolated, the nodes were too long, and the stems slender and spindling. The tissues are not properly differentiated in the absence of the short rays, the mechanical tissue is lessened, and the leaves are too thin.

The plants grown under long rays only, contained uniformly less carbohydrates than those grown in the presence of short rays. It is probable that the catabolic activities are speeded up in the absence of the shorter radiations, and most of the food is consumed as it is made. If the rays of the blue-violet region are really destructive to enzymes or retardative upon the enzyme action, then elimination of these might increase enzyme activity and cause increased metabolism.

The removal of ultra-violet radiations alone did not seem to injure the plants.

Electroculture. — Of the same class as heat and light waves are the electric waves; and they too have considerable formative influence.

[1] Schanz, F. Wirkungen des Lichts verschiedener Wellenlänge auf die Pflanzen. *Ber. d. bot. Ges.* **37**:430–442. 1919.

[2] Popp, H. W. A physiological study of the effect of light of various ranges of wave length on the growth of plants. *Amer. Jour. Bot.* **13**: 706–736. 1926.

It has been shown that the germination of many seeds is hastened by suitable electric stimuli, and for a considerable time the growth of seedlings is also accelerated. When crops of barley, wheat, beets, and other economic plants are frequently subjected to a quiet discharge of high-tension currents from wires, with many pendent points, strung over the experimental fields, it has been found by several observers that the plants grow better, come to maturity earlier, show increased productivity, and are of better quality than on control plots.

Thus, an electrified wheat plot of 3 acres yielded a crop 39 per cent greater than the control plot, sold at 7.5 per cent higher prices, and the flour was of a higher grade on account of its baking quality. Beets (for the table) on an electrified plot showed 33 per cent increase and contained an average of 8.8 per cent sugar, against 7.7 per cent on the control plot. Recent tests reported upon by the United States Department of Agriculture, however, show that there is little hope of increasing plant production by this method.[1]

Other radiations. —Ultra-violet radiations of sunlight, ranging from 291 μ to 400 μ, are probably not destructive in their action upon plants; but the shorter rays, from 185 μ to 291 μ, are destructive. They kill the epidermal cells if the leaves are exposed too long, and may cause destructive chemical changes in the enzymes and other organic compounds occurring in the living cells.[2]

The longer ultra-violet rays may have something to do with the development of vitamins in the leaves of plants, as it now seems fairly certain that the vitamins are at least in part produced by ultra-violet radiations activating the sterols. Many foods which are deficient in vitamins, but contain phytosterols can be activated and given vitamin properties by treatment with ultra-violet rays.

The X-rays are also destructive if used in heavy doses. (See fig. 61.) They are much more penetrative than the ultra-violet rays, and may cause various derangements in the chromosome mechanism of dividing cells. They may also cause hereditary modifications by such changes in germ cells.

With reference to the development of the higher plants, X-ray

[1] Briggs, L. J., Campbell, A. B., Heald, R. H., and Flint, L. H. Electroculture. *U. S. Dept. Agr. Bull.* **1379**. 1926.

[2] Kluyver, A. J. Beobachtungen über die Einwirkung von ultra-violetten Strahlen auf höhere Pflanzen. Sitzungsber. Akad. Wiss. Wien Math. *Nat. Kl.* **120**: 1137–1170. 1911.

Chanchard, A., and Mazoue, B. Action des rayons ultraviolets sur l'amylase, l'invertine, et le melange de ces deux diastases. *Compt. Rend. Acad. Sci.* Paris. **152**: 1709–1713 1911.

treatment of soaked seeds or young seedlings may cause a depression of growth during the first part of the growth period. Later on there is a partial recovery of the plant, but the final size of the plant is never as large as the control.

FIG. 61. — 20-day-old seedlings of *Helianthus annuus*. Right, irradiated; left, controls. Diagram made 16 days after irradiation. — After JOHNSON.

In the case of the sunflower, X-ray treatment of the seeds or early seedlings caused fasciation of the stems, leaves, and flowers, and other deep-seated anatomical modifications of the vascular system.[1]

Stimulative effects as the result of light X-ray treatments have been reported for the potato and some other plants, but confirmation is needed for these results.

Oxygen and growth. — A supply of oxygen about the roots of plants is usually conducive to growth.[2] Some plants have very low oxygen requirements, as seeds of *Alisma* and rice; others, like *Xanthium*, have high oxygen requirements for germination. Proper aëration of the soil is one of the prominent features of soil management, attained by drainage of the soil and plowing at intervals. In water culture solutions, aërated cultures have in some cases shown greatly improved growth. Under ordinary cultural conditions we do not need to attempt control of the oxygen supply, except to keep the soil properly drained and cultivated.

Carbon dioxide enrichment. — Under natural conditions, the slow diffusion of dissolved carbonic acid to the chloroplasts probably acts as a limiting factor on plant growth. Many attempts have been made to induce more vigorous growth, especially in greenhouses, by adding purified CO_2 to the greenhouse atmosphere. In some cases very promising increases in growth have been obtained, and carbon dioxide enrichment may prove a profitable means of increasing greenhouse-grown crops.[3] It is of course not possible to control the carbon dioxide

[1] Johnson, E. L. Effects of X-rays upon growth, development, and oxidizing enzymes of *Helianthus annuus*. *Bot. Gaz.* **82**: 373–402. 1926. See also *Amer. Jour. Bot.* **15**: 65–76. 1928.

[2] Clements, F. E. Aëration and air-content. The rôle of oxygen in root activity. *Carnegie Inst. Pub.* No. 315. Washington. 1921.

[3] Owen, O., and Small, T. Carbon dioxide investigations. *Ann. Report, Exp. and Res. Sta.*, Cheshunt, Herts. **11**: 119–122. 1925.

content of the atmosphere on a large scale for general agriculture. When flue gases are used for carbon dioxide enrichment of greenhouses, great care must be taken to wash the gases free of any injurious constituents.

Stimulants. — Some gases and volatile liquids act as stimulants, especially upon dormant organs. Ethylene, ethylene chlorhydrin, ethylene oxide, propylene chlorhydrin, and such soluble chemicals as thiourea, potassium thiocyanate, and sodium thiocyanate are being used to overcome dormancy in potatoes, gladiolus corms, and other similar dormant organs.[1] Ethylene and propylene chlorhydrin are known to increase the respiration of the organs they act upon, and ethylene possesses power to ripen, or at least hasten color development in many kinds of fruits, such as tomatoes, bananas, and green-skinned citrous fruits like lemons, tangerines, oranges, etc., by stimulating the oxidation of chlorophyll. It has been reported as useful in the blanching of celery. It seems probable that the usefulness of ethylene in ripening fruits has been overrated. The best conditions for use of these stimulants are yet to be worked out.

Radium fertilizers. — Radio-active elements have been used as fertilizers and extravagant claims made as to their value in stimulating plant growth. Applications at various rates up to enough to cost $100 per acre for the fertilizer have given results in accordance with the laws of chance.[2] Radium-containing ores are not likely to be useful in controlling plant growth, either in small or large applications.

Mechanical agents. — Pressure and tension have evident influence on the development of mechanical tissues. The encasing of a stem in a plaster cast, so that as it thickens it will compress itself, leads to changes in the structure within the zone of compression and especially just beyond the margin. Continuous tension seems to bring little if any increase in mechanical tissues, but flexure, with its alternating compression and tension, such as the wind in certain regions produces, beyond doubt increases the proportion of mechanical tissues and thickens their walls. When combined with excessive evaporation and

[1] Denny, F. E. Hastening the sprouting of dormant potato tubers. *Amer. Jour. Bot.* **13**:118–125. 1926. See also **13**:386–396. 1926.

Vacha, G. A., and Harvey, R. B. The use of ethylene, propylene, and similar compounds in breaking the rest period of tubers, bulbs, cuttings, and seeds. *Plant Physiol.* **2**:187–192. 1927.

[2] Hopkins, C. G., and Sachs, W. H. Radium as a fertilizer. *Illinois Agr. Exp. Sta.* Bull. **177**. 1915.

perhaps other unfavorable factors, the effect on bodily form is astonishing (see vol. III, *Ecology*, on stem-dwarfing).

Deformities. — Noteworthy local modifications of form are produced by the attacks of parasites, either plant or animal. When specific deformities are produced, the structures are called *galls* (fig. 40, p. 154). Just how far these are due to chemical substances excreted by the parasite, and how far to the mechanical pressure, to the punctures, or to the movements of the larvae of animal parasites, remains at present quite uncertain. Whether chemical or mechanical stimuli act upon the host, its response might be first an altered metabolism, which produces appropriate effects upon the division and course of development of the cells, resulting in the deformation of the region. Profound alterations in the relative development of the tissues and in the character of their elements accompany the deformity.

Injuries. — Injuries of various sorts call forth growth in tissues which have long passed the ordinary period of cell-division. This gives rise to a callus at the edges of the wound which tends to close it, a fact that is of great practical service in the grafting and budding so indispensable in fruit growing. Desirable sorts, too tender for a given climate, may thus be united with stocks that are hardy, but have no good qualities in their fruit.

In practice, smoothly cut surfaces are opposed and kept in close contact, with the exclusion of water and spores by wrappings and wax. The healing tissues blend, as they form at the junction, and an organic union is established, permitting the passage of water and foods freely.

If a wound be allowed to heal, the callus may give rise to new growing points, from which the regeneration of removed organs may proceed. Thus, if a root be decapitated, a new apex may be regenerated, if the cut be near enough the tip, or new lateral roots may arise that would not otherwise have been produced, or old roots may be incited to more active growth. In either case of the formation of new organs, the reaction to the wound stimulus is complicated with unknown factors named *polarity*, and with the influence of other organs called *correlations*.

Polarity. — Since the opposite ends of an egg cell give rise to unlike structures (for example, in seed plants, suspensor cells from one end and the embryo initial from the other), it is assumed that the two hemispheres are unlike, even though no structural differences are visible. This is expressed by the term *polarity*, after the analogy of the invisible

differences in the two ends or poles of the magnet. A like polarity must be imputed to all other cells, its progeny, so that the embryo initial, when it develops, produces at the one end a root and at the other a shoot. Later in life, any piece of the shoot cut away from the rest shows a tendency to produce shoots at the apical end and roots at the basal end, when put under conditions to regenerate lost organs. The conception of polarity in the cells is thus extended to aggregates of cells of any size, because they show such differences at the apical and basal ends. Polarity may be the result of metabolic gradients in the axial tissues of the plant, or more specifically to gradients of oxidation-reduction potentials in the meristematic and differentiating regions of growth.

Correlations. — The term *correlation* designates the reciprocal influence of organs. Of this little is known beyond the fact that the suppression or the removal of one organ exercises a marked effect upon some or all of the remaining ones. Many examples might be cited, but no adequate explanation of the effects can be given; while frequently correlation is related to the utilization of the food by one organ so that another is suppressed, yet it is known that at least some of them are not due merely to differences in the food or water supply, or to like conditions. Examples will make clear what is meant by correlations.

Quantitative correlations. — In the axil of each cotyledon of the bean there is present a bud, neither of which develops into a shoot unless the main axis is cut off or prevented from developing. If one desires sweet peas and such plants to continue flowering, it is necessary to cut away the older flowers or the young pods, so as to prevent the formation of fruit. If this is done, the plants go on flowering till frost, whereas their season is quickly over when allowed to set seed. The gametophyte of ferns is short-lived, as a rule; but if the fertilization of the egg be prevented, its life may be prolonged for months, and it proliferates, forming archegonia again and again. The possibility of shaping a tree by judicious pruning, and of increasing the production of fruits by orchard trees in the same way, rests upon like reactions.

Qualitative correlations. — Correlations are not merely quantitative, as the above examples might seem to imply; they are also qualitative. That is, the whole behavior and even the structure of an organ may be altered according as other organs are present or absent. Thus, the central axis of most conifers is strictly radial in structure and in branching, while the lateral branches are distinctly dorsiventral. But if the terminal shoot be cut away, one (or more) of the laterals may become erect, losing entirely the dorsiventrality, and becoming radial like the leader. The aërial shoots of the potato, which bear foliage leaves and flowers, are very different from the subterranean ones, which bear the scales and tubers. But if the aërial shoots be cut away,

some of the subterranean shoots will turn up into the air, become green, and develop foliage and flowers as though never inclined to be subterranean. The sporophylls of certain ferns, notably *Onoclea*, are entirely different in aspect from the nutritive leaves, and have so many sporangia crowded on the surface that they seem entirely covered. If all the nutritive leaves be cut away, leaves that ordinarily would have become sporophylls will then become foliage leaves and bear no sporangia. In like manner the tendrils of the pea leaf may be made to develop into leaflets.

In all these cases transformation is possible only before the primordia have gone too far in any determined course, though the point at which new influences may affect them is very different in the different cases. Usually the stimulus must be applied very early, while the primordia are still undifferentiated. Many of the problems of regeneration are complicated by these phenomena of correlation, if they are not wholly determined by them.

3. IRRITABILITY

External agents. — It is a matter of common observation that the size and form of plants is affected by the conditions under which they are grown. The luxuriance of weeds in a neglected garden, in contrast with their stunted forms on a dry roadside; the rich green corn of a high prairie, in contrast with the yellowish and starved plants on a wet clay field; the thrifty trees of a park, in contrast with the struggling and dying ones along a paved street, can hardly fail of notice by the most unobservant. These differences show clearly that the complex of conditions external to the plant profoundly affects its internal processes. As all functions center in the living stuff, protoplasm, the conclusion is that protoplasm is *sensitive* to the various agents that act upon it (or *irritable*); that is, that it *reacts* or *responds* to these by altering its behavior in some way. In that event the agent producing the reaction is a *stimulus*. These three topics, stimulus, response, and sensitiveness or excitability, require consideration.

Variety of stimuli. — The forces that act upon any plant are many, and varied in direction and intensity; and their combinations are almost infinite. Consider a tree, growing in a city park. Every day the light which falls on it varies both in direction and in intensity from hour to hour, and is almost lacking at night; furthermore it varies from day to day and season to season. The temperature is hardly the same from one hour to another, and in our climate occasionally changes 10° C. within twice as many minutes, while the seasonal

changes range over some 70° C. The humidity of the air shows like hourly, daily, and seasonal fluctuations, and the tree may be thrashed by a parching wind or wrapped in a dripping fog.. A gentle shower, torrential rain, or hail may fall upon it within the hour; and with a change of season it may be weighed down by sleet and snow. The underground parts suffer less extreme variations of temperature than the top. The water content of the soil swings from the drought of summer to the saturation of late winter and spring, and the solutes vary more or less in concentration with the rains and evaporation. Combine all these in as many ways as possible, and some idea is obtained of the variations in external conditions which may affect the plant.

Adjustment.[1] — To many of these a plant must be able to adjust itself on pain of death, and suitable response to others is advantageous. The plant is indeed a self-adjusting mechanism, whose reactions are oftentimes more delicate than those of our own bodies, with all their special senses and complicated sense organs. Thus, many a tendril is sensitive to a mechanical stimulus which we cannot perceive, even by the tip of the tongue, the portion of the body most sensitive to contact; and some plants distinguish differences of illumination which are inappreciable to the eye. On the whole, it is perhaps fair to say that plants are more responsive than animals. The plant has mostly to take what comes and make the best of it; the animal often takes shelter from unfavorable conditions or migrates to a gentler climate.

Intricate relations. — It is extremely difficult to disentangle the complex of forces acting on a plant and to assign to each its special influence. Out of them all only a few have yet been isolated. What are known as general or formative stimuli, namely, the totality of physical conditions, external and internal, which determine the general course of development and consequently the form of the plant as a whole or of any particular organ, furnish especially intricate problems, because it is so difficult to alter only one condition experimentally, or to evaluate the influence of those which cannot be controlled. Experience is showing, too, that so-called special stimuli, *i.e.* those which act locally, such as gravity, light, heat, etc., are interrelated, and their effects are unexpectedly interwoven. No phase of plant life requires more careful experimentation and more caution in inference than the study of stimuli and the responses to them.

[1] This term must be understood as if it were applied to a steam engine or a dynamo, both of which adjust themselves automatically to their "load."

Definition. — A stimulus is any change in the intensity or direction of application of energy which produces an appreciable effect upon living protoplasts. Of course when no appreciable effect is produced, the energy may differ neither in amount nor form from that which does arouse a reaction; and effects may be produced which are not perceived because improper tests are applied. A stimulus, thus, has no absolute value; it implies not a definite amount of energy measured in physical units, but merely enough applied suddenly enough to call forth a reaction as revealed by some arbitrary test. Therefore, what is a stimulus under certain conditions, is not a stimulus under others.[1] Nor need the stimulus arise or act outside the plant as a whole. It may originate in one part and act upon an adjacent part, even in one protoplast and act upon another. These stimuli, in one sense external and in another internal, are most difficult to study. They are in part and perhaps wholly the occasion for the reactions that are called autonomic, or less properly "spontaneous."

Kinds. — Stimuli may be classified for convenience as mechanical, chemical, and ethereal. Under mechanical stimuli are grouped those which depend upon mass movements, resulting in contact, impact, friction, pressure, etc., upon the plant. For lack of definite knowledge of the nature of gravitation, the stimulus of gravity may be conveniently included here, since it depends upon mass attraction and induces mass movements. Under chemical stimuli are included those whose action depends on their chemical quality — their composition and molecular structure — rather than on their mass. Ethereal stimuli comprise those propagated as vibrations in the ether and distinguished according to the length of the waves as light, heat, and electricity.

Modes of reaction. — The action of a stimulus results in stimulation or excitation, and this may or may not lead to an observable reaction, depending upon the state of the protoplasm and the means used to detect a change in its behavior. Thus, immediately upon excitation a change in the electrical condition of the protoplast occurs, but this does not manifest itself to our senses, unless the stimulated region and an unstimulated one are put into electrical connection with the poles of a sensitive galvanometer (fig. 62). At the same moment a contraction

[1] No sharp distinction can be drawn between the stimuli which are followed by a prompt and easily observable response and those external agents whose very gradual change has no early apparent effect, but produces ultimately some deviation from the usual course of development. In the broad sense both are stimuli, but the term is usually applied only to the former, in which sense it is here defined.

of the protoplasts occurs, and this may or may not be apparent. It expresses itself by a change of position in the leaf of *Biophytum* (fig. 62) or of *Mimosa* because there is at the base of the leaf a cushion of cells, whose lower ones, on account of the stimulation, exude some of the water that kept them tense more readily than do the upper ones. Again, upon stimulation there may be a change in the rate or amount of

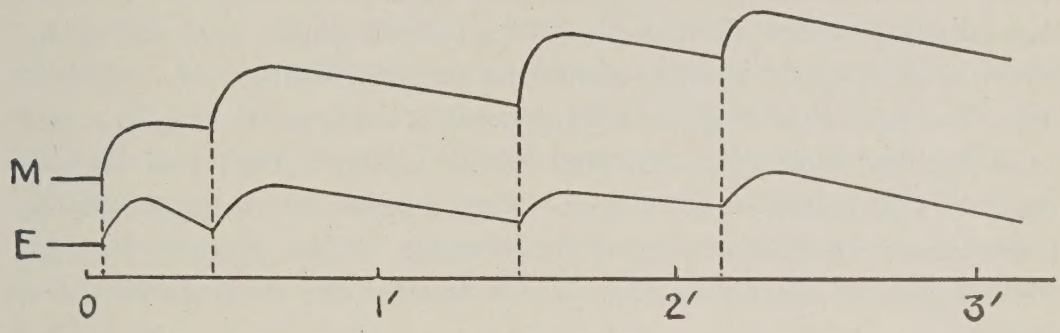


FIG. 62. — Records of simultaneous mechanical (*M*) and electrical (*E*) response in *Biophytum:* the figures are seconds; dotted lines show the moment of application of a stimulus, and the solid lines the deflection of the leaflet or of the galvanometer needle. — After BOSE.

some function or, more rarely, a change in the character of a function. Thus, the protoplasm of a gland may be caused to secrete more or less rapidly than before, or the protoplasm in a growing cell may have its growth accelerated or retarded. Further, a gland may have the character of its secretion profoundly altered by excitation, or a part not growing may have its cells set again into active division and growth.

Sensitive plants. — The fact that certain plants, having a special mechanism, respond to a stimulus quickly by a mechanical movement has given them an undeserved reputation as " sensitive plants " *par excellence;* but they are not really more sensitive than others. Whether a plant exhibits movements or not depends on whether it has an appropriate mechanism to permit the protoplasmic contractions to propel it through the water, or the changed turgor to displace an organ, or the changed rate of growth to cause a curvature. Movements, then, are favorable for a study of sensitiveness merely because they are obvious reactions that can often be observed without apparatus. They do not signify unusual sensitiveness, nor does immobility imply its lack. *Every plant responds appropriately to a sufficient stimulus, and every plant is therefore a sensitive plant.*

Propagation of the excitation. — The reaction specially observed is not usually the only one. It may be only one of a series, and curvature, resulting in movement, is most likely to be merely the *end* reaction.

Thus if a primary root of a bean be set horizontal, the first reaction occurs instantly and in the very tip of the root, but it is not visible; only after a half an hour or more, at a distance of 2–3 mm. from the tip, does a growth reaction set in that starts to turn the root tip downward. Between the first reaction and the last there must have been a series of changes, each of which was a reaction to a preceding stimulus and a stimulus to a succeeding reaction. By a rough analogy the process may be compared to the tumbling of a row of blocks, each falling by reason of the impulse from its predecessor and impelling its successor to fall. The push that displaced the first one is the primary stimulus, and if the last were properly connected mechanically, it might, for the end reaction, ring a bell or fire a gun. Such a series of reactions is often spoken of as the transmission of the stimulus. More properly it is the propagation of the excitation. It is equally the propagation of a reaction.

None of these phrases nor the above analogy should be understood to require that the reactions in a series are necessarily alike, nor is the end reaction the only one to which the term properly belongs, though it is usually so applied unless the contrary is indicated.

Perceptive region. — The region where the first reaction occurs is often called the receptive or perceptive [1] region, particularly if a later and obvious end reaction occurs at another place. Since in animals a similar localization of sensitiveness for special stimuli marks the peripheral portion of sense organs, these regions in plants, especially when very circumscribed, may be looked upon as sensory organs of the simplest sort.[2] Regions of this sort, sensitive to gravity and light as stimuli, will be described later (pp. 268, 286). In the great majority of cases, however, perception is not strictly localized, and the condition resembles rather that in the diffuse senses of animals, like those of touch and temperature.

Transmission. — Special tracts, the nerves, exist in almost all animals, along which the excitation is progagated, but nothing at all comparable has been found in plants, though this claim has been made more than once. The most that can be said is that propagation is more rapid lengthwise than crosswise of the cells of a tissue and in some tissues is easier than in others. Presumably the propagation is from

[1] These words are used in a figurative sense, and the last must not be understood to have its usual psychological implication.

[2] Here again it is necessary to point out that in no sense is consciousness implied.

protoplast to protoplast by way of the slender threads, *plasmodesmen*, that connect them, traversing the walls. It is not at all certain that there are not other more mechanical means of transmitting the disturbance that eventuates in movement.[1]

Responsive region. — Corresponding to the perceptive region, the place where the final reaction occurs is called the active or responsive region. Of course it is not more active or responsive than the intervening regions; but attention is fixed on it as the seat of the selected reaction. Thus, in the root above referred to, the perceptive region is in the root cap, the excitation is propagated backwards through several millimeters of meristematic cells to those in the phase of enlargement, and the region of most rapid growth is the responsive region, because there the growth rate is unequally affected on the upper and under side, and so a curvature appears in that zone, which turns the tip downward again.

Mechanism of reaction. — Consideration of even one such curvature shows that the nature of the reaction is in no way determined by the nature of the stimulus, since the same stimulus produces a number of reactions differing entirely from the end reaction, curvature. When many movements are studied, this feature appears most strikingly, for it is seen that the same stimulus may produce curvatures in exactly opposite directions in different parts, such as a root and a shoot, while different stimuli may call forth identical responses. Further, stimuli of the same sort at different intensities may call forth opposite reactions. The mode of action is determined in fact by the mechanism concerned. Just as an electric current may ring a doorbell, start an engine, or explode a mine, according to the mechanism at the end of the wire; so an electric current may shorten a stamen, drop a leaf, or curve a tendril, according to the mechanism set into operation in the plant. Yet probably there is some effect, fundamentally similar in each case, which works out to a different final result, just as, in the comparison, the magnetizing of an iron bar underlies the varied results.

[1] The "nerves" of leaves are so called only by analogy, as the correlative terms, "veins" and "ribs," indicate. They probably have nothing to do with transmitting an excitation in ordinary cases, though some recent observations allege the contrary. Bose's claim that the phloem strands are the "nerves" of plants, and that the cross walls are synaptic membranes in the same sense as the end plates between animal nerves and muscle fibers cannot be accepted. The phloem cells may transmit disturbances, but only by general protoplasmic conductivity.

Tropic, nastic, taxic movements. — In some cases, however, the stimulus in a measure controls the reaction. A stimulus that acts upon plants from a definite direction, and consequently from one side, may determine by that fact the plane of the consequent curvature, provided the organ be physiologically radial, *i.e.* capable of response in any plane. Such curvatures are called in general *tropic* and the phenomena *tropisms*. To these terms is often prefixed a word indicating the stimulus which calls forth the tropism, as geotropism (*gē*, the earth = gravity), phototropism (*photos*, light), etc. (see p. 283). When a curvature evoked by either a uniform or a one-sided stimulus is restricted to a single plane by the bifacial structure of the organ, the curvatures are called *nastic*, and the phenomena *nasties*. This term is also applied to like curvatures due to unknown ("internal" or "inherent") causes. Thus we have epinasty and hyponasty, photonasty, photepinasty, etc. (see further, p. 245). In the organism capable of locomotion, a one-sided stimulus may determine the direction of creeping or swimming. These phenomena are *taxic*, collectively *taxies*, and individually chemotaxy, phototaxy, geotaxy, etc., according to the stimulus (see p. 250).

Energy relations. — Not only is the mode of reaction independent of the kind of stimulus, but its energy is disproportionate to the amount of energy expended in excitation. The stimulus, therefore, cannot be the sole cause of the reaction, though the two stand related to each other apparently as cause and effect. On the unexpected pricking of the finger, little energy is expended; the sudden jerking away of the hand involves many times as much. Somewhere this energy must have been released and applied; and this is one reaction of the series, whose final one was movement. So in the plant, stimulation often involves a mere fraction of the energy expended in the final movement; it is released, presumably from the protoplasm or some part of it that is particularly unstable, and is applied to the work. If this be so, the chemical changes (metabolism) ought to be different in a stimulated and unstimulated organ.

This hypothesis, however, has not yet been verified experimentally. Reinvestigation of the one case in which such a result was reported has produced a conflict of evidence.

Another hypothesis, that stimulation results in molecular strain only, from which there is gradual recovery, sufficiently accounts for fatigue (see next paragraph), but does not account for the disparity in energy between stimulus and reaction, the existence of which its advocates merely ignore or deny.

Fatigue, tetanus, and summation. — After an organ is stimulated once and the response occurs, the original state is presently regained, and the organ is ready to respond again as at first (fig. 63). If several stimuli follow, each before complete recovery, the responses are of less extent than before. This effect is described by the term *fatigue*, and in many cases the responses gradually become smaller and smaller until they cease entirely. When the stimuli recur very frequently, the

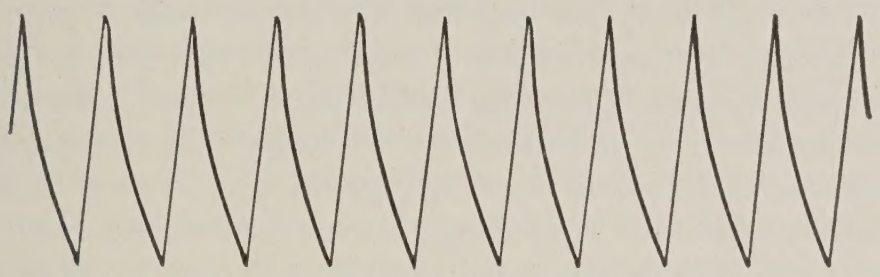


FIG. 63. — Uniform electrical response in radish to repeated stimulation. — After BOSE.

responses become for a time combined, so that the organ assumes a fixed position unlike the unstimulated one. This quite resembles the condition of a muscle in tetanus, as can be seen by comparing the records in fig. 64. After a period of tetanus, however, the reactions cease until rest from excitation permits recovery. If stimulation, too brief to produce the end reaction, be repeated at proper intervals, the separate effects become combined and suffice presently to call forth the end reaction. This *summation of stimulation* seems to be a sort of tetanic piling up of the earlier excitations of the series, which finally becomes sufficient to transmit its effects to the active region.

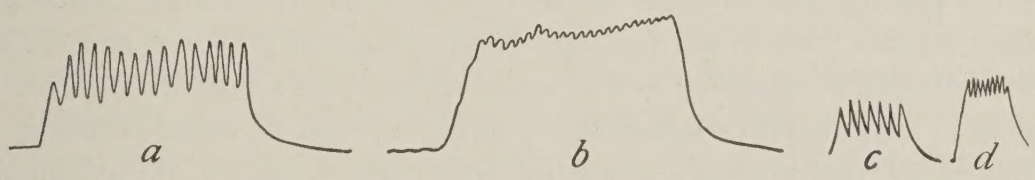


FIG. 64. — Records of tetanic contraction in muscle (*a*, *b*) and in style of *Datura* (*c*, *d*): *a*, *c*, incomplete; *b*, *d*, more complete. — After BOSE.

Reaction time. — Some time elapses between the beginning of stimulation and the end reaction, and this is appropriately called *reaction time*. Whereas in animals this is usually measured by a fraction of a second, in plants it is much longer, occasionally a few seconds, but often minutes or even hours. This tardiness is due not so much to a low degree of sensitiveness, for the first reaction (perception) takes place almost instantly, as to slow propagation and especially to the sluggish-

ness of the mechanism of growth. By contrast, turgor mechanisms usually respond quickly. Naturally the reaction time is made up of the perception time (a small fraction of a second), the transmission time (the rate varies commonly from 0 to 4 cm. per second), and the growth time, which is far the greater part of the whole period.

Presentation time. — In order to produce any reaction a stimulus of given intensity must act for a definite time, called the *presentation time.* For the primary reaction this is extremely brief — practically instantaneous. But end reactions, especially those due to growth, require some minutes or even an hour or more. Thus, roots must be kept horizontal for 15–30 minutes or even longer (depending upon the plant and its condition), in order that gravity may cause a curvature. This means, apparently, that the excitation must reach a given pitch through continuous or summated stimulation, before it can be propagated to the active region and affect the growth mechanism. Once that pitch is attained, the end reaction will follow; and if the initial stimulus cease to act, it will follow as an *after effect.* If the intensity of the stimulus be increased, presentation time is correspondingly shortened (within limits, the ratio is inverse).

Excitability. — To obtain a reaction it is not enough that a stimulus act upon a plant. The protoplasm must be in a certain condition, or excitation cannot follow. This is clearly recognized when it is said that a " dead " plant no longer responds to stimulation as before. It was once said: " The dead organism is ' dead ' merely because it has lost its irritability "; but this is true only by an extension of the term *irritability* beyond its usual sense. Closer study reveals the fact that many agents that do not produce death temporarily abolish or reduce or even exalt excitability. When protoplasm is in a condition of excitability, it is also in a condition to carry on well its usual activities; irritability therefore is associated with other normal physiological qualities covered by the term *tone.* One experiences the feeling of well-being and vigor; it comes when all the functions of the body are proceeding properly. So under favorable conditions the plant's functions are all effective and this *tonic condition* may be assumed as the norm,[1] the result of the combined responses to many simultaneous external and internal stimuli. Retardation or acceleration of particular functions may then be brought about by the intensification or weakening of

[1] Note that this is not a fixed or well-defined condition; it is merely the usual, the ordinary; and it is assumed purely for convenience.

particular stimuli of this complex, or by the application of unusual ones.

Loss of irritability. — Excitability may be diminished or abolished temporarily by a dose of anaesthetics, like chloroform and ether, certain other functions being also interfered with. The precise mode of action is not known, but the anaesthetic action is accompanied by a change in permeability, the cells becoming more permeable.[1] Other substances decrease permeability, and these show antagonism to those substances which increase permeability. After a time the effect passes away and tonic irritability is regained. By a larger dose irritability may be permanently abolished (that is, it kills), while by a smaller dose it may become heightened. Various narcotics act in a similar way. Substances that kill are usually called poisons; really they are poisons only in certain doses. Their modes of action are doubtless as different as the poisons themselves.

In the following sections, the foregoing general principles will find specific illustrations in the movements of locomotion, in the nastic and tropic curvatures of various organs, in the displacement of leaves by motor organs, and in the effects of stimuli upon form. It is important that the principles just set forth be constantly referred to and kept in mind in reading these sections.

4. NASTIC CURVATURES

Epinasty and hyponasty. — A somewhat more specific action of external stimuli upon plant behavior is to be found in their effects upon the rate of growth on the two faces of bilateral organs, such as thalli, foliage leaves, bud scales, perianth leaves, etc. It is very common to find that such organs grow at different rates on the two faces, so that they are distinctly curved thereby. Thus, in their earliest stages, the leaves grow fastest on the back or outer side, so that the inner face is pressed close to the axis, and as they usually outgrow it, they curve together over it in a protective fashion, forming a bud. The scales, especially, long maintain this form, as the longitudinal section of any bud will show. Later, the relative rate changes; the inner face grows more rapidly than the outer, and the bud opens because the curvature carries the leaf or scale away from the axis. Thalli often show the same thing; the upper surface may be so tense from greater growth that the thallus is tightly appressed to the ground. Such curvatures are described

[1] Osterhout, W. J. V. *Injury, Recovery, and Death in Relation to Conductivity and Permeability.* Lippincott. 1922.

briefly by the terms *epinasty* or *hyponasty*, according as the greater growth is on the upper (inner) or lower (outer) face. The greater number of these nastic curvatures are due to unknown (internal?) causes, but some have been found to be reactions to external stimuli (paratonic). The former are not unlike those autonomic curvatures of radial organs described as nutations (p. 208), only in this case the bilateral structure of the organ determines that the nutations shall be in one plane only. The latter are also allied to tropisms, but differ from them in that not the direction from which the stimulus acts but the structure of the organ predetermines the plane of the movement. When temperature is the exciting cause we speak of thermoepinasty and thermohyponasty; but if light causes the differences in growth we speak of photepinasty or photohyponasty.

Light and temperature. — Examples of paratonic nastic curvature are seen when light and temperature act as stimuli upon foliage and flower leaves, and less plainly in tendrils. Temperature changes are especially effective with the perianth leaves of tulip,[1] crocus, snowdrop, colchicum, and other plants whose blossoms appear very late in the autumn or very early in the spring. In the crocus a rise of half a degree suffices to bring about a curvature that opens the flower; while the tulip can be made to open and close as many as eight times in the course of an hour by raising and lowering the temperature. Tendrils respond to a temperature change, whether a rise or a fall, by curving in one direction only, the upper side being stimulated to accelerated growth. In this they differ from the perianth leaves cited, for in these a rise of temperature tends to accelerate growth on the inner face and thus to open the flower, and a fall to accelerate growth of the outer face and so to close the flower. Very many, perhaps the majority of foliage leaves, show nastic curvatures in response to alterations in temperature and light as long as the petiole is still capable of growing; finally curvature ceases and the fixed light position of maturity is attained. Such bending movements remind one of the photeolic movements executed throughout life by leaves that have motor organs (see p. 255). Among flowers those most strikingly responsive to light are the heads of some Compositae, such as the dandelion. Here the flowers and the bracts about the flower cluster, the involucre, curve so as to close the head when the light is diminished, as in cloudy days, and to open it in sunshine.

[1] Andrews, F. M. The effect of temperature on flowers. *Plant Physiol.* **4**: 281–284. 1929.

In countries where the climate is equable it is possible to select plants whose flowers open at particular hours of the day on account of light and temperature stimuli, and by planting them in a circle to have a sort of floral clock. Naturally it is not very reliable.

Gravity. — Nastic curvatures are also produced in plants in response to gravity, which, however, usually coöperates with or antagonizes the light reactions. In all cases the stimulus at work may be indicated by the prefix, as noted previously. Thus photonasty and thermonasty are the two main nastic curvatures. In the case of gravity, we would have geohyponasty or geoepinasty.

Mechanism. — In all these curvatures the mechanism of response is the same. The growth of the outer or inner surface is accelerated, as can be shown by making equidistant marks upon the two faces and measuring the changes. This observation shows, too, that under frequent stimulation the total growth is much greater than it is under uniform conditions.

5. LOCOMOTION AND STREAMING

Locomotion limited. — Locomotion is restricted among plants to the simplest forms (with a few exceptions to those that are unicellular), and to the gametes, especially the male gametes, of the multicellular plants. The reason for this is doubtless to be found in the restriction of freedom to move imposed by the cell wall — in effect a sort of strait-jacket — in which the protoplast incases itself. Even when the protoplast moves, as it often does, within this case, its movements do not bear against the outer medium and therefore do not propel it about. The only exception to this restriction occurs in those plants whose wall is perforate; then the protoplasm protrudes through the opening so as to operate against the outer medium, or in a few cases as in the diatoms, it excretes mucilage forcibly against the medium or the substratum and so pushes itself slowly along.

Rate. — When the protoplast changes its shape suddenly, quick swimming and darting movements result; when slowly, the movement is perceptible only because magnified by the microscope. In the very swiftest movements the absolute translation is small, say 50 mm. per minute; and in the sperms of ferns, which under the microscope seem to be going fast, the rate is only 0.1 to 0.2 mm. per minute. Measured relatively, as in terms of size, and taking account of the resistance of the medium, the translation is seen to be very rapid. The very fast human

runners cover about 50 times their own length (100 yards) in 10 seconds; the swarm spores of *Ulva* can travel 100 times their own length in the same time; and the spiral sperms of a fern (*Nephrodium*) can do 50 to 100 times their length (as coiled) in 10 seconds (fig. 65).

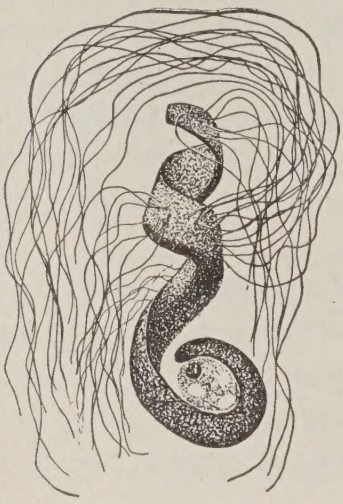


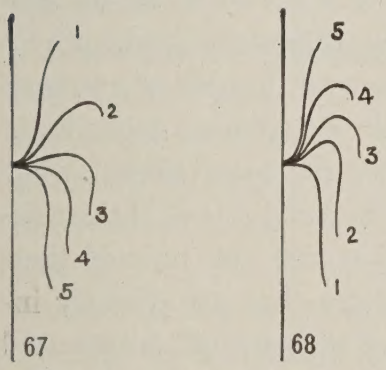
FIG. 65. — Sperm of *Nephrodium* with fagella. — After YAMANOUCHI.

Amoeboid movements. — The slow movements are a kind of creeping, and are of two sorts, amoeboid and excretory. Amoeboid movements (so called because characteristic of *Amoeba*, a genus of infusoria) are found rarely among plants, being known only in the plasmodia of Myxomycetes, a group of organisms with so many animal characters that they are often included in the animal kingdom. The plasmodium is a naked mass of protoplasm (sometimes like a thin cake, often a richly anastomosed network), which during its vegetative period lives in wet places among decaying wood, leaves, etc. The creeping is accomplished by the protrusion of marginal lobes of the protoplast along one side, possibly by means of changes in surface tension, and toward these lobes the rest slowly flows. In this way the whole mass advances in a definite direction, which is frequently changed and is subject to control by external agents. Thus, by varying the temperature, the moisture, or the illumination, the plasmodium may be made to creep in one direction or another. It is thermotactic, phototactic, and hydrotactic, but its response to these stimuli differs with its own stage of development. Whereas during a considerable vegetative period it avoids light and drier places, later it creeps out from the substratum and ascends to drier and exposed situations, where it produces sporangia with a casing and framework of cellulose and a multitude of spores.

Excretory movements. — Excretory movements are executed by some diatoms and desmids, and those of *Oscillatoria* and *Spirogyra* are probably of this sort. The diatoms and desmids forcibly excrete mucilage through slits or pores in the wall against the substratum (a glass slide, the wall of an aquarium, the bottom of a pool, or the surface of a water plant) over which they creep slowly with a majestic and mysterious motion, which is not yet fully understood (see also p. 255).

Ciliary movement. — The more rapid movements are called ciliary, because executed by the lashing of slender threads of protoplasm through the water, in which alone such organisms can move. The motile threads are known as *cilia* or *flagella*.[1] They arise from different places on the protoplast, often at the pointed apex or along a band, where the special organ which produces them, the blepharoplast, is located (fig. 66). The flagellates (unicellular organisms of uncertain relationship), bacteria, the zoöspores and gametes of certain algae and fungi, and the sperms of bryophytes, pteridophytes, and cycads, exhibit ciliary locomotion. The cilia are so slender, and when magnified sufficiently their movements are so rapid, that the details of the strokes are difficult to follow. In the thicker cilia of infusoria the forward stroke (fig. 67) consists of a progressive bending, which begins below the free tip and advances to the base, where it is most powerful. At the moment of greatest efficiency (fig. 67, 2), the curve bears against the water like the blade of an exaggerated spoon oar (though, of course, the cilium is not flattened). The return stroke (fig. 68) is slower and consists of a reverse and somewhat different curvature, advancing from base to apex.

FIG. 66. — Swarm spore of *Hydrodictyon*, with two cilia arising from a blepharoplast with nuclear connections. — After TIMBERLAKE.



FIGS. 67, 68. — Diagrammatic representation of successive positions (as numbered) of cilia of *Urostyla grandis;* 67, in forward stroke; 68, in recovery. — After VERWORN.

Cause. — The cause of these repeated lashings is completely hidden. They continue for a time and then cease. Though they cannot be initiated, they can be stopped or modified in rate by appropriate stimuli, and their duration can be prolonged. Thus, if zoöspores of algae be released in light, they may swim about for a few hours, then attach themselves and germinate. But if they be kept in darkness, the swimming may continue for two or three days,

[1] No constant distinction can be made between cilia, which are typically short, hairlike, and numerous, and flagella, which are long, whiplike, and few (1–4) for each cell. Yet a cell sometimes has a single cilium, or two, and flagella are numerous on the sperms of ferns.

until the zoöspore seems entirely exhausted and perishes without settling down.

Taxies. — The direction of swimming may also be controlled by external agents. The phenomena of directed locomotion are comprehensively called taxies, and with a prefix, designating the directive agent, we have phototaxy, thermotaxy, chemotaxy, etc. These responses, apparently simple, are really very difficult to interpret, and experiments, seemingly quite conclusive, may lead to false inferences through the operation of some overlooked factor. Thus, if a dish containing zoöspores of algae be placed on a window ledge so that one side is more brightly illuminated than the other, the swarm spores will be seen to accumulate on the side with brighter light, and this movement was described at first as a positive response to light. Later it was found that the droplets in an oil emulsion would behave in the same way because of the previously unnoticed differences in temperature, making convection currents in the dish. Two factors were therefore involved and more rigid tests were needed to demonstrate phototaxy.

Chemotaxy. — Chemotaxy has been most extensively investigated, but is not yet fully elucidated. If a soluble crystal be introduced into water undisturbed by currents, the molecules gradually diffuse from its surface in a constantly enlarging sphere; or if the water be the film under a cover glass, in an increasing zone. By using a glass tube drawn out to a very fine capillary and closed at one end, liquids of any sort may be used. A short capillary is filled with the solution and placed on a microscope slide with its open end under the cover glass. Slow diffusion takes place from the mouth, while the behavior of the organisms is watched under the microscope. As a rule the rate of their movement is not affected, except by substances that are directly injurious. It appears that the directive effect of such stimuli is exercised in two different ways.

1. **Orienting reaction.** — In the first case, the direction is altered because the organism, in response to the stimulation, orients itself, so that with continued movement the body will be carried toward or away from the source of the diffusing molecules. It is assumed that this orientation is determined by the unequal or one-sided action of the molecules, the end (less probably the flank) toward the source being most powerfully affected, whereupon the creature turns, and according as it brings the anterior or the posterior end toward the source of stimulus, and swims, it will approach or recede from that source.

2. Recoil reaction. — The second case is quite different. The movements of sperms and zoöspores are too rapid to be followed easily; but if large and slow-moving organisms are observed, they may be seen to swim about quite indifferently, passing in close proximity to the crystal or capillary tube from which the molecules are diffusing, without showing any tendency to swim towards it. But when they reach by chance the limits of the diffusion zone, they suddenly reverse their direction and back away, as though they had encountered an obstacle and had rebounded from it. Such recoil movements are called apobatic reactions. This reaction is repeated at every side, and having once chanced to swim into the diffusion zone, they are imprisoned within it, because the attempt to pass out of it results always in the reaction of recoil. So, as more and more are thus caught, there is an accumulation within the diffusion zone, as though it were a trap. Not all substances, however, permit the first accidental entry, for the recoil may be produced at the attempt to enter this zone, while any such organisms placed within it would be free to swim out without recoil. In such a case the final result is the accumulation of the organisms in the regions outside the diffusion zone. Besides the reaction of recoil, there are accompanying minor reactions which cannot be discussed here.

Attraction and repulsion. — Many different substances have been tested with respect to chemotactic control. Some prove to be attractive, some indifferent, and some repellent. Equisetum sperms are attracted by malic acid only, while the sperms of ferns are attracted by both malic and maleic acids. Fumaric acid is not attractive to fern sperms, but is, along with malic acid, for the sperms of Isoetes. Among the bryophytes, sugar and protein solutions have been found effective in attracting sperms. That responses occur to substances that are never met in nature, as well as to those that are not foods, and further, that they do not prevent the organisms from coming to serious or even fatal injury, indicates that chemotaxy depends upon some fundamental property of the protoplasm and is not a mere adaptation to secure special ends, however well it may occasionally serve such a purpose. In many cases a substance which is attractive at a low concentration proves to be repellent at a higher. In such a case the question arises whether the repellent action is due to the chemical constitution of the stimulant or to the osmotic pressure of its solution. As the latter seems to be the reason for the action in certain cases, the phe-

nomenon is named *osmotaxy*. It has not yet been sufficiently investigated, but is in many ways parallel to chemotactic irritability.

Amount effective. — The amount of a substance which can act directively upon motile organisms is infinitesimal. Thus it was found that a minute capillary into which the sperms of a fern crowded, contained, all told, less than three hundred-millionths of a milligram (0.000000028 mg.) of malic acid. Of this, certainly, only a very small fraction could have reached any one of the sperms. Yet relatively the amount is not at all insignificant; for the estimated weight of one of the sperms is only ten times greater than the total weight of the acid, and if only 1/100,000 of the total acted upon a sperm, the ratio would be 1 : 1,000,000, which is still 10 times the ratio of a minimum effective dose of morphin for the human body.

Weber's law. — The phenomena of chemotaxy offer an excellent illustration of a general law of response known as *Weber's law*. If a fern sperm is swimming in water, it will be diverted toward a capillary containing malic acid whose concentration is 1 part in 100,000 of water. But if it is brought into a solution too weak to evoke a response, say 1 : 200,000, it is so affected by the enveloping acid that it does not respond unless the solution in the capillary is 30 times as strong as that by which it is surrounded, *i.e.* 30 : 200,000. If again the concentration of the acid in the medium be raised, say from 1 : 200,000 to 1 : 100,000, the concentration of the stimulant in the tube must be 30 times greater, *i.e.* 30 : 100,000, in order to evoke response; and so on. It appears from this that a sensitive organism becomes adjusted to a constant non-directive stimulus, and then is unresponsive to an intensity of one-sided stimulus of the same sort, to which in the unaccustomed state it reacts. Thus accommodation is really a lowering of irritability toward a particular stimulus. The noteworthy point is that it is a proportional lowering; for, after each adjustment has occurred, it requires a definite increase in intensity (in this particular case a large one — 30 times the constant) to call forth a response. Some ratio of this kind, whether it be an increase of 3 times or 30 times the constantly acting stimulus, has been found to hold good for many forms of response and in many sorts of organisms. In all cases the law is valid for moderate stimuli only; an intensity is soon reached where it ceases to express the facts.

The law was formulated in 1834, with reference to touch and sight. It has been stated lately thus: "The smallest change in the magnitude of a stimulus

which will call forth a response always bears the same proportion to the whole stimulus."

Aerotaxy. — One form of chemotaxy has received a special name, *aerotaxy*, which signifies that the air, or more exactly the oxygen of the air, is the excitant. Certain forms of bacteria are motile only when they are in contact with oxygen, and cease to move when they are deprived of it. In so far, this also might be due merely to respiratory disturbance, just as many functions cease when no oxygen is supplied. But these forms also swim in the direction from which the oxygen is diffusing, and accumulate about its source. Such forms, if evenly distributed under a cover-glass, soon desert the center and gradually accumulate at the edge, where the O_2 is diffusing into the water. These species, motile in oxygen, can be used as indicators of photosynthesis, because O_2 is a by-product. Engelmann employed such oxygen-sensitive bacteria to detect the photosynthetic action of chloroplasts many years ago.[1]

Ionic stimuli. — All chemotactic reactions to substances that dissociate in water probably rest upon the specific action of the various ions and molecules present in the solution, and attempts have been made to correlate the action of the various salts and acids. But the phenomena are too complex to permit satisfactory analysis yet; and since undissociable substances also act as stimuli, it is probable that the undissociated molecules, as well as the ions, have a stimulating action in many cases.

Phototaxy. — Phototaxy is particularly characteristic of those organisms that have chlorophyll, such as the zoöspores of algae and the ciliated colonial algae like *Volvox*, *Eudorina*, etc.[2] That they swim towards light of moderate intensity is not to be doubted; but it has been very difficult to determine whether this response is due to the direction of the light rays, or to the fact that one region is more brightly illuminated than another. Accumulation certainly occurs in regions of moderate light, with avoidance of the more shaded or the more brightly illuminated portions. The most exact of the recent studies of *Volvox* shows that its orientation is controlled by the relative intensity of the illumination on different sides of the colony, and as it swims with a definite pole forward, swimming after orientation causes it to move nearly parallel with the rays, some deflections from this course being due to certain minor disturbing factors.

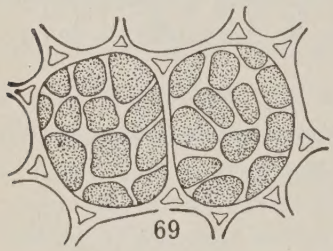
[1] Harvey, E. N. Photosynthesis in absence of oxygen. *Plant Physiol.* **3** : 85–89. 1928.

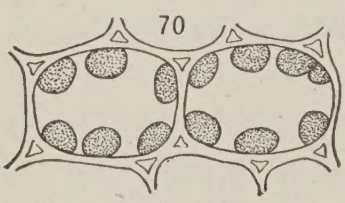
[2] Some fungus swarm spores also are sensitive to light.

In phototaxy, as in chemotaxy, organisms respond both by orientation and by recoil, though, so far as known, the latter is much less common. The light waves vary in action according to their length, the reds and yellows, though the brightest, being quite unstimulating, whereas the blues are most effective. Yet this gives no clew to the real nature of the excitation or of the organs by which it is perceived.

Geotaxy. — Certain organisms have also been found to be geotactic. This property is quite distinct from others; for organisms that respond alike to other stimuli, such as light and oxygen, may react differently to gravity, the one being positively, the other negatively geotactic. Upon such irritability may depend the ability of the creatures to rise or sink through the water on occasion.

Motion of cell organs. — Not unrelated to the movements of free-swimming organisms that have been described are the movements of organs of the cell which take place within the limits set by the wall. Such, particularly, are the movements of the chloroplasts and the nucleus. The chloroplast movements are known to be in part responses to light stimuli. Certain algae of the genus *Mougeotia* (*Mesocarpus*) have a single plate-like chloroplast, which lies in the axis of the cell, facing the incident light, when this is of appropriate intensity. But if the light becomes more intense, the plate rotates until the edge is presented to the light. The numerous rounded chloroplasts of seed plants, mosses, etc., alter their distribution and their shape according to the illumination (figs. 69, 70). This suggests a sort of escape from too bright light, an idea that agrees with what is known of the intensity of light required for photosynthesis (see p. 132). Yet the arrangement is seldom as regular or complete as it is sometimes described, and effective protection from light is secured mainly in other ways. Aside from their own amoeboid movements the chloroplasts are subject to displacement by movements of the protoplast, as in streaming (p. 255).





FIGS. 69, 70. — Two leaf cells of a moss (*Atrichum undulatum*) seen from above: the chloroplasts in 69 in epistrophe; in 70, in apostrophe. — After SCHIMPER.

The nucleus also changes its position in the cell " spontaneously " or in response to certain stimuli, notably to wounding. Nothing is known as to the significance or mechanism of such movements.

Streaming. — In very many active cells a streaming movement of portions of the protoplasm has been observed. In some cases there is a constant movement in one direction round and round the cell, a movement called rotation. This is seen in *Elodea* cells. In other cases, an irregular and reversible movement which is called circulation occurs, as in *Tradescantia* stamen hair cells. The layer closest to the wall does not participate in the movement, and though the chloroplasts, when any are present, are not necessarily involved, they are often swept along when they lie deeper. The rate of the motion varies with temperature and with other conditions that affect the general activity of the protoplasm, and the movement may be entirely stopped by appropriate stimuli. Nothing is known as to the causes or the effects of these movements, though they are extremely common and perhaps universal. The idea that they facilitate the more rapid distribution of foods and solutes in the cells and so hasten osmotic transfer of materials would be more plausible were streaming less common and vigorous in those cells, *e.g.* in hairs, where such a process seems of slight importance.

In some diatoms the protoplasm partly protrudes through a longitudinal median slit (the raphe) in the valves, and streaming movements in this outer belt, reacting against the water or the substratum, propel the cell slowly in the direction opposite to the outer streaming. The counter-stream, of course, moves within the cell wall.

Surging movements of the protoplasm in the coenocytic hyphae of *Mucor* and other fungi have been seen, but their causation and significance are unknown.

6. TURGOR MOVEMENTS

Motor organs. — In a considerable number of plants thin-walled turgid cells are so arranged that the position of the organ of which they form a part depends upon the relative turgor of these cells. In most cases the organs are leaves, either foliage or flower leaves, and the structure is such that the *motor organ* curves only in one plane, the distal part rising or falling with the variations of turgor. Examples of these motor organs are afforded by the leaves and leaflets of the Leguminosae and the Oxalidaceae, by the stamens of *Berberis*, and by the stigmas of *Mimulus;* they are also found in a considerable number of families allied to the Berberidaceae and Scrophulariaceae.

Structure. — The leaves of Leguminosae are usually much branched, and the primary motor organ, when present, is located at the base of the main petiole. In many cases there are also motor organs (second-

ary) at the origin of the secondary petioles, and if the leaf is ternately compound the petiolules or stalks of the leaflets are motor organs. Thus *Mimosa* has primary, secondary, and tertiary motor organs (fig. 71); but the red and sweet clovers have only one set, the stalks of the leaflets. The motor organ consists of all or a portion of the petiole or petiolule, modified by changes in the position of the vascular bundles and by an excessive development of the parenchyma of the cortex. Through the greater part of the leaf stalk the vascular bundles lie at some distance from the center, surrounding a distinct pith, and within a cortex of moderate thickness. In the motor organ, however, they approach one another so closely that there is scarcely any central pith, and they form a shaft, elliptical or kidney-shaped in section. Outside, the cortex is correspondingly larger, and its cells are usually somewhat different from the rest. As a whole the motor organ is sometimes thicker than the other part of the petiole, but it is quite as likely to be smaller; in all cases, however, the relative increase of the cortex in cross section gives the impression of a cushion of parenchyma.[1] In this region the cells are rather regular in form, approximately cylindric, and with smaller intercellular spaces than in the nutritive regions. Intercellular spaces are present, however, at the junction of three or more cells.

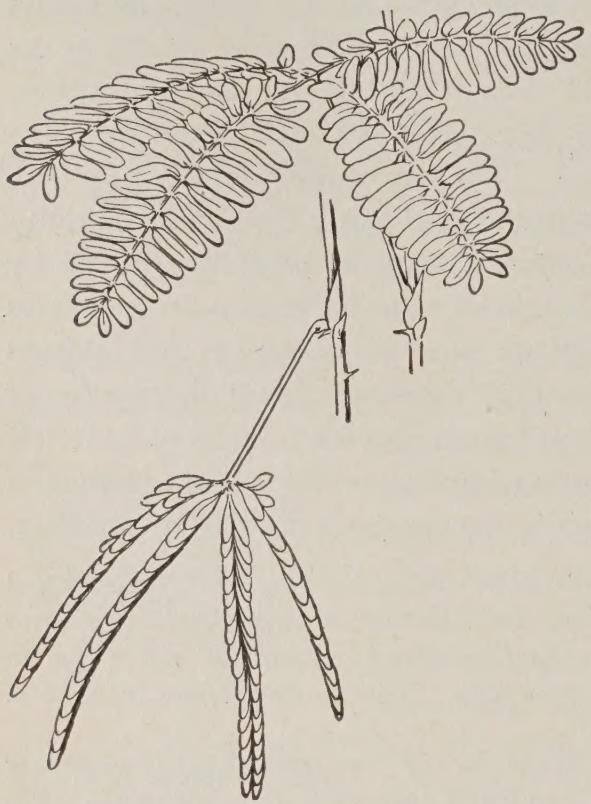


FIG. 71. — Leaf of *Mimosa* in open and closed positions.

Mechanism. — It is evident that the central position of the vascular bundles permits flexure more readily than if they were scattered and more peripheral; while the peripheral position of the thin-walled cells of the cortex is such that any variation in their turgor will produce a curvature, the side with less turgor becoming concave, since its cells

[1] This is the reason for a technical name applied to the motor organ, the *pulvinus*.

no longer oppose fully the turgid cells of the opposite side. Correspondingly, the parts beyond the curving motor organ will be displaced by it. These turgor variations, due to modified permeability, being usually restricted to the upper and lower sides of the motor organ, the distal parts are moved up and down. Since the relaxed cells may recover turgidity and the turgid cells become flaccid, the notable feature of all such movements is that the changes in the cells are *reversible;* whereas the cell changes involved in growth are *irreversible* (or soon become so).

The motor organs of stigmas and stamens are essentially similar to those of foliage leaves, but simpler, since vascular tissues are slightly or not at all developed, and almost the whole tissue is parenchymatous.

Autonomic movements. — The variations in turgor are sometimes autonomic, that is, determined by causes unknown and apparently internal to the plant, but more commonly they are controlled by external stimuli. Autonomic movements are not at all uncommon, but they are mostly too slow to be observed easily without apparatus, and, when sought, are often masked by more obvious movements (see p. 261). The classical and almost the only striking example of easily seen movements is offered by *Desmodium gyrans,* whose lateral leaflets (fig. 72) are constantly rising and falling under favorable conditions. These movements, sometimes uniform, but usually jerky, are not very rapid, for a complete up-and-down movement requires 2–4 minutes. The fall is more rapid than the rise (for example, 45 sec. as against 70), and as the turgor variations tend to fluctuate regularly to right and left of the vertical plane, the tip of each leaflet describes a narrow ellipse. The reason for these movements is unknown, nor are they known to be of any value to the plant. Under unfavorable conditions they cease, but the plant may still be able to respond to external stimuli like others about to be described.

FIG. 72. — Leaf of telegraph plant (*Desmodium gyrans*), natural size: *l*, *l*, lateral leaflets which show autonomous movements; the terminal leaflet in the depressed position. — After PFEFFER.

Paratonic movements. — The terminal leaflet of *Desmodium gyrans,* like leaves of other members of the bean family, exhibits *paratonic*

movements (*i.e.* those due to special stimuli, not tonic; opposed to autonomic). Moreover, some plants whose leaflets ordinarily exhibit only paratonic movements may make autonomic ones under exceptionally favorable conditions. Thus it would seem that there is no fundamental difference in the two, and when the precise stimuli that initiate the movement are discovered, autonomic movements may all be relegated to the paratonic category.

Turgor movements due to external stimuli are numerous and easily observed, but except in a few striking cases they are not rapid enough to be seen by watching for the brief time. The stimuli initiating the movements are of the most varied character; contact, gravity, and changes of light and temperature being the most common.

Contact movements. — If the stamens of the barberry (*Berberis*) be touched near the base at the time when they are shedding pollen, they suddenly fly up and inward, carrying the anthers close to the stigma. After a short time they resume their former position against the petals. The filaments of the Cynareae, a tribe of Compositae, shorten instantly on being touched (the reaction time is less than 1 sec.), dragging the coherent anthers quickly down over the style, whose hairs scrape out the pollen like a pipe cleaner. In *Centaurea americana*, this contraction continues for 7–13 seconds, and after a minute the rest position is again reached.

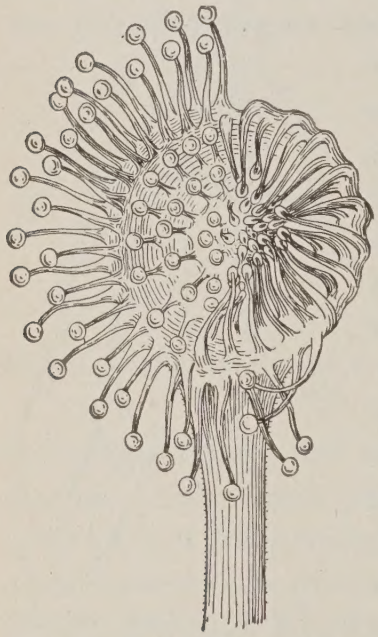


FIG. 73. — Leaf of sundew (*Drosera rotundifolia*) with half of the tentacles inflexed from stimulation. — Adapted from KERNER.

Probably the best known of the rapid contact movements are those of the species of *Mimosa* and *Biophytum*, the "sensitive plants." In *Mimosa* the leaflets are carried by the motor organs forward and upward until the upper faces are pressed together, while the primary motor organ drops the whole leaf (fig. 71, p. 256). Another famous example is the quick closure of the "fly-trap" of *Dionaea* (figs. 42, 43, p. 157). Here the motor organ lies along the central rib, between the two lobes of the leaf, and when an insect touches one of the three sensitive bristles on either face, these lobes shut together quickly like the jaws

of a trap, and their interlocking teeth prevent the prey from crawling out easily. After a time the superficial glands pour out a secretion containing an enzyme that digests the proteins, and these are absorbed and utilized as food. After several days the trap again opens. Somewhat slower movements are made by the " tentacles " of *Drosera* (fig. 73). When an insect is entangled in the viscid secretion at the tips of these leaf lobes, its struggles furnish a stimulus which results in the incurving of all, until it is completely enveloped in their secretion, which then changes character, becoming digestive, and so prepares the proteins for absorption (see p. 159).

Gravity movements. — Gravity cannot act as a stimulus unless the plant be displaced. If a potted bean plant be turned upside down or laid on the side, in a few hours the motor organs become curved so as to bring the leaves again into the usual position, or as near to it as possible.

Photeolic movements. — The most striking movements are the regular ones produced by motor organs under periodic stimulation by variations in the intensity of light (and temperature). These have been known under the misleading name of " sleep movements," because they are notable at nightfall. However, they have no similarity whatever to the relaxed position assumed by animals in sleep, nor do they bring any recovery from fatigue. On the contrary, the nocturnal position is one of precisely as much strain as the diurnal one, since the resistance of the motor organ to bending is measurably the same; and even the position is as likely to be erect as drooping.

Technically they have been called *nyctitropic* movements, but as the curvature is not a tropic one this term is objectionable, and the more so as the movements are quite as much associated with day as with night. They are best called photeolic (*i.e.* light variation) movements, because the illumination is chiefly responsible for them, though corresponding fluctuations in temperature accompany the changes in light and sometimes coöperate in setting up the movement.

Photeolic movements consist of a rising or falling, a forward or backward movement, of the entire leaf and (if the leaf be compound) of all the leaflets as well; or the leaflets alone of a compound leaf may exhibit such movements. The change in the leaves of the common purslane (figs. 74, 75) will make clear the general character of these changes of position, which are executed by differences of turgor on opposite sides of motor organs appropriately situated. Inasmuch as

the changes in illumination are not sudden (in nature), it should be expected that the movements would not be restricted to morning and nightfall. In fact it can be shown that there is really a slow variation, so that in the brightest hours of the day the blades reach their highest or lowest position, the opposite being attained in the maximum darkness. As the changes in the intensity of the light are most marked at dawn and at dusk, the changes of position are then most rapid and so attract attention.

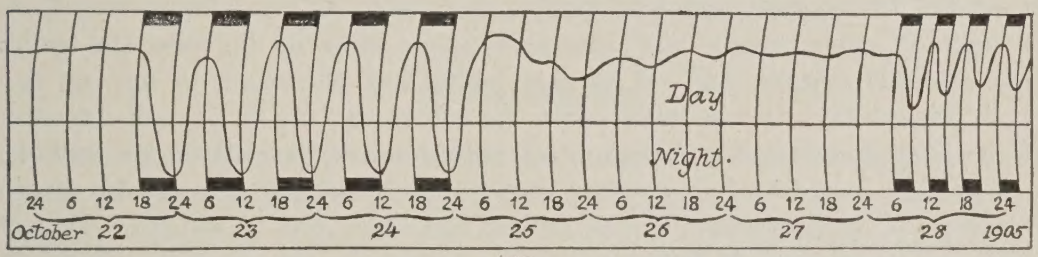
FIGS. 74, 75. — Shoot of the purslane (*Portulaca oleracea*), photographed from identical position at 2 P.M. (74) and at 8.30 P.M. (75); note that the older leaves show little change of position. — From photograph by LAND.

Persistence.—To these periodic variations in light the plant becomes habituated, and even if they are not allowed to occur, as when a plant is kept in continuous darkness or continuous light, the movements continue, with diminishing amplitude, for a considerable time (3–5 days) before they cease entirely. The normal periodic stimulation seems to have impressed upon the protoplast a rhythmic variation in turgor, so that it cannot at once cease the customary action even when no stimulus demands a reaction (fig. 76).

When these movements are ceasing, there come to view similar ones which are usually masked by the photeolic reactions. These, however, are autonomous; they are much less extensive and have a much shorter period than the others. When sought, they can be observed even in the presence of the photeolic movements. They consist of a pendulum-like swinging of the leaf or leaflets, up and down (somewhat as in *Desmodium*, fig. 72; see also fig. 77), whose advantage and effects are alike obscure.

Advantage. — The benefits of photeolic movements have been variously imagined. They have been supposed to prevent injury to the

leaves by frost, since the folded position diminishes radiation; or to prevent the formation of dew, so that transpiration may begin promptly in the morning. The difficulty with the first of these ideas is that frost does not occur in the regions where Leguminosae, which exhibit them more strikingly than any other family, most abound; furthermore, a temperature approaching o° C. would render response impossible. The second explanation involves the assumption, which may be correct, that transpiration is a valuable function which the



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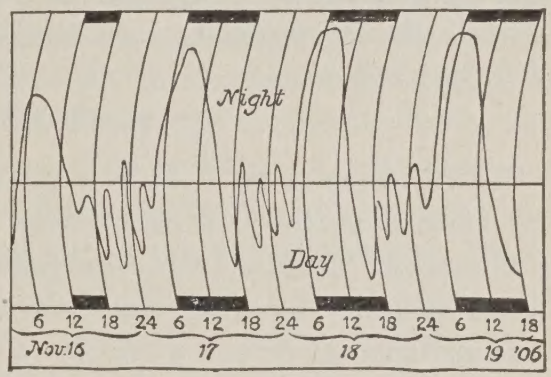


FIGS. 76, 77. — Autographic records of leaf movements: dates and hours of the day are given below; 12 noon, 24 midnight; the horizontal median line represents the line the recording point would have described had the leaf remained quiet, moving neither toward the diurnal (*day*) nor the nocturnal (*night*) positions; the black strips mark the periods of darkening, which have no relation to the natural alternation of day and night; 76, photeolic movements of leaf of *Albizzia lophantha;* after a period of constant illumination the plant was subjected to 6-hr. periods of alternating darkness and light, then to continuous light, and finally to 3-hr. periods of alternate darkness and light; note the persistence in light (Oct. 25–27) of the movements, which gradually disappear; 77, photeolic and autonomous movements of leaf of *Phaseolus vitellinus*, the latter restricted to the reversed periods of illumination (6 P.M. to 6 A.M.); note the lag of the response in the former. — After PFEFFER.

plant promotes, instead of a danger that menaces its very life. It is difficult to conceive the significance of these movements in terms of welfare, and it is quite possible that they have none.

Other stimuli. — Changes in temperature, which often coincide and coöperate with changes of light in producing photeolic movements, may act alone, and, when sufficient, call forth like responses. Severe injury, even when wrought without mechanical disturbance, as by burning with a lens, will also stimulate the motor organs to curvature. So will a variety of other stimuli.

Growth movements and turgor movements. — The intimate relations that exist between turgor and growth, as well as the suddenness of their response under favorable conditions, make it possible that the first curvature of ten-

drils (see p. 278) is due to quick alterations in the turgor of the cortical parenchyma. If this be true, the turgor curvature is followed promptly by unequal growth, to which irreversible process the more permanent and more important of the tendril movements are due. Their behavior will therefore be discussed in connection with growth movements. Indeed it is not improbable that turgor changes underlie all such movements, though they are not apparent.

In many plants whose leaves have no well-defined motor organs there exist slight modifications of structure looking in the same direction, with movements of less extent than those executed by well-developed motor organs. Moreover, there are to be found similar movements in young leaves that have no trace of motor organs, but these movements cease by the time the leaves have attained mature size. (Compare young and old leaves in figs. 74, 75.) Doubtless growth, that is, irreversible changes in the size of the cells, as contrasted with the reversible changes produced by turgor, cause these movements.

From the foregoing it is evident that no hard and fast line can be drawn between the displacements due to turgor and those due to growth. In fact there are all gradations between them. Therefore, the separate treatment must not be permitted to establish in the mind too sharp distinctions; for distinctions are valuable chiefly as conveniences to the memory; they have usually slight basis in nature.

7. TROPISMS

Growth curvatures. — It is a matter of common observation that the various parts of a plant have definite positions. If they are mechanically displaced, the usual position often is resumed after a time by curvature. Again, if some external force acts upon them from an unaccustomed direction, a curvature may result, restoring the customary relations so far as may be. Some of these curvatures have been considered; namely, those that are due to changes of turgor. But a much larger number are due to inequalities of growth, because few plants have such a structure as to permit turgor variations to move an organ. On the contrary, every plant has some part where growth is either in progress or can be initiated, and consequently a curvature can be induced, if by appropriate mechanisms the amount or rate of growth can be modified locally. Practically all plants have such mechanisms, which are set into operation by various external stimuli. It will be most convenient to consider these *tropic* curvatures according to the stimulus that induces the reaction.

Parallelotropic and plagiotropic organs. — Observation shows that in certain plants the main axes respond to a tropic stimulus by placing themselves parallel to the direction from which the stimulus acts, while other parts, such as the branches or leaves, set themselves at a definite

angle to the line of the stimulus. Other plants may place even the main axes at an angle to the stimulus. This difference of behavior is expressed by the terms *parallelotropic* and *plagiotropic*, applied to the organ concerned.

Because responses to tropic stimuli lead so often to the erect position of axes, such axes were first called *orthotropic* organs, and those set at some angle to the erect position were called plagiotropic, with reference merely to position. No confusion can arise from the substitution of the more specific term *parallelotropic*, and the use of plagiotropic in a somewhat modified sense, to indicate a position at an angle to the parallelotropic position.

(1) Geotropism

The stimulus. — No force acts so constantly and so equally in all parts of the earth and in all situations as gravity. It might be expected, therefore, that it would have some influence upon the position that the parts of plants assume. If there were nothing more to be observed than that the main stems of so many plants in all countries are directed away from the center of the earth, this would suggest the agency of some general stimulus. But it is easy to observe that as soon as a plant stem which usually grows erect is placed in horizontal position, curvatures occur in the younger parts that again direct the apex upward, though the older parts are unable to erect themselves. Fallen trees, and corn or other cereals beaten down by wind and rain, offer many examples, and the simplest experiments suffice to demonstrate the main facts; namely, that gravity is the stimulus, and unequal growth on opposite sides of stems or roots the end reaction.

The first demonstrative experiments were conducted by Knight at the beginning of the last century, by affixing boxes to the rim of a wheel, which could be rotated either in the vertical or the horizontal plane, and planting seeds in these boxes. When the seedlings appeared on the vertically placed wheel, they seemed to have quite lost their way, growing in any direction in which they happened to be pointed when they broke through the soil; and some did not even emerge. On the horizontal wheel, however, no difference was apparent when it was rotated slowly; but when it was turned rapidly enough to introduce a considerable centrifugal acceleration (" centrifugal force ") the usual position of the axes was changed, the stems which would normally grow erect tending to direct themselves toward the center of the wheel, and the primary roots, which usually grow downwards, growing toward

the periphery; and these tendencies were the more pronounced the more rapid the rotation.

This mode of experimentation is universally used when one wishes to equalize or modify the action of any one-sided stimulus. In all such experiments it is essential to arrange the plants so that the only factor in their environment that is altered is the direction from which the stimulus acts. The clumsy wheel has been replaced by the modern *clinostat*, a disk to which potted plants can be conveniently attached and capable of rotation in any plane, continuously or intermittently, at a very even speed [1] by strong clockwork or by a water or electric motor. The centrifuge is a modification whose disk is driven at a high speed when centrifugal acceleration is to be compared with gravitational.

Parallelotropic organs. — The behavior of parallelotropic and plagiotropic organs differs in certain particulars. The former will first be considered. Parallelotropic stems in responding to gravity curve so as to erect their apices when displaced. Primary roots, which are usually directed straight downwards, when displaced respond by turning the tip toward the earth. These responses, in quite opposite directions, arise from an identical original stimulus. By some mechanism within the plant body the end reaction is made different. It is convenient to distinguish the difference by assuming some difference in the sensitiveness. So the special term *positive geotropism* or *progeotropism* is used to designate the property by which the growing point is directed toward the center of the earth, and *negative geotropism* or *apogeotropism* that by which the tip is turned away from it. There are four possible explanations. The curvature might be due (*a*) to unequal retardation of growth along both sides; or (*b*) to unequal acceleration of growth along both sides; or (*c*) to an unchanged rate of growth on one side with either acceleration or retardation on the other; or finally (*d*) to simultaneous retardation on one side and acceleration on the other. It has been determined that usually, in both stems and roots, gravity accelerates growth, but the segments are unequally affected according to position (case *b*). In the one case (apogeotropism), the lower side is caused to grow more rapidly than the upper; in the other (progeotropism), the upper side grows more rapidly than the lower. How this difference in action is brought about is quite unknown.

Course of curvature. — The course of curvature in a parallelotropic stem continuously stimulated by being laid horizontal shows an inter-

[1] Otherwise any exact experiments may be vitiated by errors due to unequal stimulation, a common fault with makeshift clock clinostats, which suffice, however, for elementary demonstrations.

esting example of "after-effects." The reaction time is usually some hours in length. When the apex has reached the erect posture again, it might be supposed that it would go no further. On the contrary, it is carried past the vertical, responding to the excitation set up some hours before. Being thus carried beyond the position of equilibrium, it is stimulated to a reverse curvature, and this also, by reason of continued stimulation during the long reaction time, may again carry the tip past the vertical; thus, only by a series of pendulum-like swings is the position of equilibrium attained. The successive positions of the stem of *Impatiens* shows the way in which such a stem erects itself (fig. 78). It shows also that the curvature begins in the region of most active growth and gradually affects less active regions, becoming permanent finally as the tissues of the growing region most remote from the apex cease to grow.

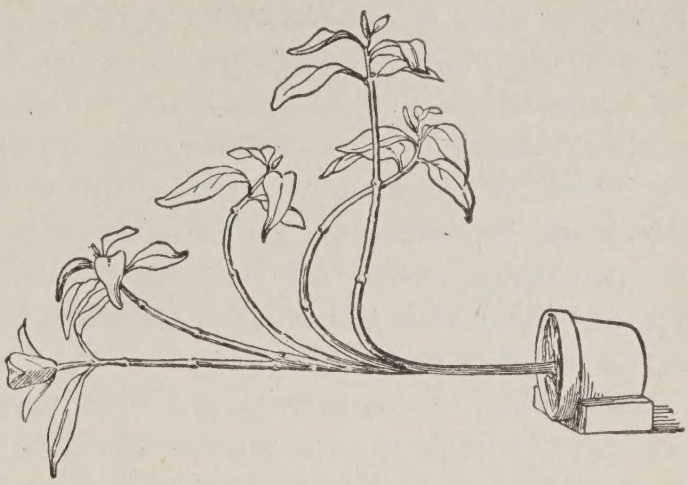
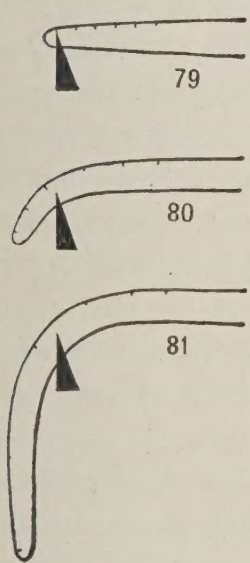


FIG. 78. — Successive positions, from photographs, of *Impatiens glanduligera* in erecting itself from the horizontal. — After PFEFFER.



FIGS. 79–81. — Geotropic curvature of a root of *Vicia faba:* 79, placed horizontal; 80, seven hours later; 81, twenty-three hours later. — After SACHS.

That the curvature appears in the region of most active elongation is clearly shown by the behavior of certain roots. If a suitable one be marked at intervals of 1 mm. and then fixed in a horizontal position, it will be found after some hours that curvature is taking place in the third and fourth of these divisions; after twenty-four hours it is easy to see that the second and third divisions have grown most, though the chief curvature still persists in the fourth division that was growing most rapidly (figs. 79–81).

Presentation time. — It is not necessary to continue stimulation until the reaction appears. In other words reaction time is longer than presentation time. These periods are, of course, very variable. The shortest presentation time

recorded for geotropic curvature is 2–3 minutes (cut shoots of *Capsella*, hypocotyls of *Helianthus*, and peduncles of *Plantago*). In many plants it is 15–25 minutes; in less sensitive plants it is double or treble this, or even extends to several hours. Both periods are greatly influenced by temperature. Thus, a seedling of *Vicia faba*, having at 14° C. a presentation time of 70 minutes and a reaction time of 120 minutes, had these periods at 30° C. respectively 10 minutes and 48 minutes. The longer the stimulation, other things being equal, the more marked the curvature; from which it is evident that there is an increase of the excitation with continued stimulation, and thereby the end reaction becomes more marked.

Summation. — Contrariwise, it should be expected that stimulation too short to result in curvature would not be without effect. That it does produce excitation is shown by the fact that if a plant be placed alternately horizontal and erect, each period of stimulation being shorter than the presentation time for that particular plant, and the interval of rest shorter than is needed for recovery, curvature will finally occur. Evidently this is a cumulative effect; yet it is not a summation of the total successive excitations that occur during the times of horizontality, but only of the residual excitation, the difference between the excitation and the recovery. For, if a suitable plant be placed horizontal for 30 minutes continuously, the reaction curvature is more pronounced than if it be so placed for ten 3-minute periods at 10-minute intervals. Clearly, while erect, the preceding excitation is slowly disappearing, and if the interval before the next stimulation is too long, recovery will be complete and no evidence of the excitation will appear in the form of curvature.[1] In such experiments, therefore, it is necessary to apportion properly the intervals of rest and stimulation.

Rotation. — From the above considerations it will be evident that when a plant is rotated in the horizontal plane on a clinostat, its failure to execute any curvature is not at all due to a lack of excitation, for while the side *a* of the stem is passing through quadrant *A* of its rotation (fig. 82), quadrants *a* and *c* are under stimulation almost as though for a corresponding time the stem were at rest. But these sides remain under stimulation for less than the presentation time and so the

[1] It has been suggested that during the periods of no stimulation a counter-excitation is set up; but simple recovery from excitation seems sufficient to account for all the facts known. The process is apparently analogous to recovery from fatigue.

excitation does not suffice for the end reaction. When side *a* has passed into quadrant *C* of its rotation and *c* into *A*, any residual excitation from the former position is balanced by excitation that would lead to a contrary reaction. All the while, therefore, the plant is under excitation, which is the greater the more opportunity there is for summation; and if the responses were not contrary the one to the other, curvature would show itself. The net result upon the rotated plant is that growth is at first accelerated as compared with a control plant rotated in the vertical plane; but long-continued rotation leads to fatigue and no response.

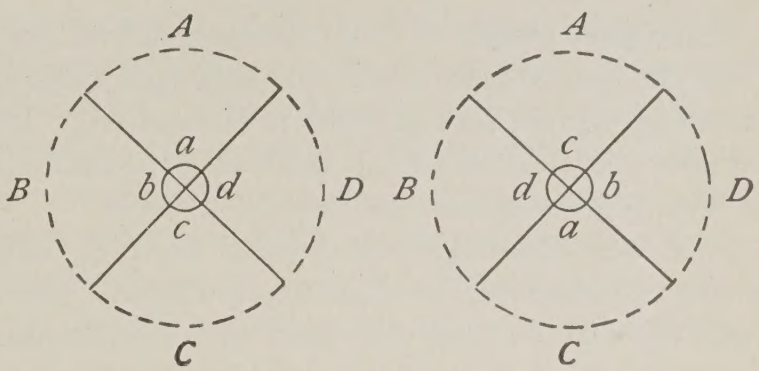


FIG. 82. — Diagram: for explanation, see text.

Position of equilibrium. — In order that a parallelotropic axis be in a position of stable equilibrium with respect to gravity, it must not only be parallel to its direction, but the stem must be erect and the root pointed downward. There is a polarity which must be conserved. Though the strictly inverted position for either roots or stems is one of little stimulation or possibly of none, it is a position of such instability that the slightest deviation leads to stimulation, which results in decided curvatures and recovery of the normal position. Much study has been given also to the position of maximum stimulation. The general results are most strongly in favor of a 90° deviation from the normal, as against 135° or any intermediate angle.

Variable intensity. — By comparing centrifugal acceleration with that due to gravity, it has been shown that it produces the same curvatures. So while it is not possible to alter appreciably the intensity of gravity, it is possible to vary this corresponding stimulus. Experiments in this line show that as the centrifugal acceleration is increased or diminished, the reaction time is shortened or lengthened, but whether proportionately or not is uncertain.

Thus, in earlier experiments with a root of *Vicia*, whose usual reaction time at 1 g[1] was 90–100 min., when the centri-acceleration was equal to 35–38 g,

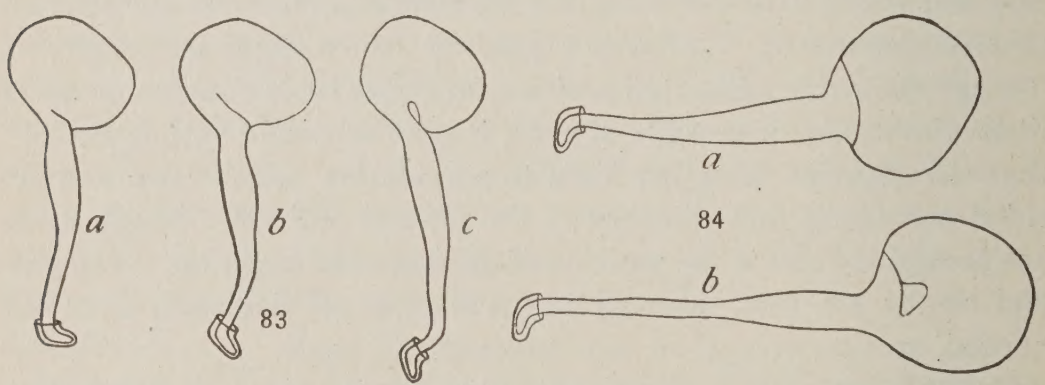
[1] 1 g = the normal acceleration due to gravity.

the reaction time was scarcely more than halved (45 min.); and when it was reduced to 0.001 *g*, the reaction time was barely quadrupled (6 hr.). In some other experiments, however, a root of *Vicia*, which reacted in 8 min. at 1 *g*, reacted in 0.25 min. with 27 *g*. Here the ratio is 32 : 27, a change in reaction time nearly proportionate to the change in stimulus.

Perceptive region. — It is extremely difficult to locate beyond question the exact region where the geotropic stimulus is perceived. In stems perception does not seem to be localized. If the statolith theory of geo-perception be true, it takes place probably in the starch sheath, a layer of cells around the vascular cylinder.

The most thorough experiments, however, have been made upon roots, and these seem to show that perception takes place mainly in the very tip, within a zone little more than a millimeter long, including the root cap. Indeed, the inner portions of the root cap itself are believed to be the cells most concerned. But the results also show that the growing region has some perceptivity.

This conclusion rests upon evidence derived mainly from three modes of experimentation: (*a*) *Decapitation.* Cutting off the terminal millimeter or two leaves the root still capable of weak response, after recovery from the shock. (*b*) *Mechanical deformation.* If root tips are made to grow into glass



FIGS. 83, 84. — Roots of *Vicia faba* with tips in glass slippers: 83, *a*, *b*, *c*, three stages in the curvature of the same root, 0 to 20 hours; 84, *a*, *b*, two stages of the same root; *b*, 18 hours after being placed in position *a*. — After CZAPEK.

slippers (figs. 83, 84), or against a glass plate, so that the terminal millimeter is bent at right angles to the body of the root and therefore can be placed in the position of stimulation while the rest is not (or *vice versa*), responses show the dominance of the excitation at the tip over that in the growing region; but the conclusion that the tip alone is perceptive is not warranted. (*c*) *Rotation.* Experiments in which the roots are fixed on a centrifuge, deviating 135° from their normal position, permit responses to be varied at will, according to the extent of the root tip beyond the axis of rotation. In all

cases, if the stimulus to the growing region is to determine the response, it must be several times greater than is needed at the tip. Anatomical facts, in connection with the statolith theory of geoperception, support the physiological evidence above cited (fig. 85).

Theories of geoperception and response. — Several explanations have been offered to account for the ability of plants to perceive displacement of their bodies with respect to the forces of gravitation and to respond to such stimulation. The best known of these theories is the statolith starch theory which was proposed by Haberlandt[1] and Némec[2] about 1900. A great number of investigations have centered about this theory, but without either proving it, or discrediting it seriously.

In addition to the statolith theory, there is a chemical theory which proposes that chemical changes are induced in stems, roots, and other geosensitive organs;[3] these changes are believed to be more concerned with the reaction of the organ than with the perception of stimulus. Finally, there is the recently proposed hydrion theory,[4] which relates the response of the plant to the difference in ionization of proteins prevailing in positively and negatively responding organs. Each of these theories will be considered briefly in the following sections.

Statolith theory. — In its original form as proposed by Noll, this theory was purely speculative. It postulated in the protoplasts of perceptive cells minute vacuoles, beyond the limits of microscopic vision, filled with a fluid in which there lay granules of slightly greater specific gravity, that would fall to the bottom of the vacuole, whatever position it occupied, and rest against the cytoplasmic membrane bounding it. In the normal position of parallelotropic organs this would lead to no excitation; but if the cells were displaced, the granules

[1] Haberlandt, G. Über die Perception des geotropischen Reizes. *Ber. d. bot. Ges.* **18**: 261–272. 1900. See also Zur Statolithentheorie des Geotropismus. *Jahrb. wiss. Bot.* **38**: 447–500. 1902.

[2] Némec, B. Die Perception des Schwerkraftreizes bei den Pflanzen. *Ber. d. bot. Ges.* **20**: 339–354. 1902.

[3] Schley, E. O. Chemical and physical changes in geotropic stimulation and response. *Bot. Gaz.* **56**: 480–489. 1913. See also *Bot. Gaz.* **70**: 69–81. 1920. These papers present the bibliography of the chemical theory, also.

[4] Small, James. A theory of geotropism with some experiments on the chemical reversal of geotropic response in stem and root. *New Phytol.* **19**: 49–63. 1920. See also *Proc. Roy. Soc. London* B. **90**: 349–363. 1918; *New Phytol.* **19**: 208–209, 209–210, 210–212. 1920; *New Phytol.* **20**: 73–81, and 116–123. 1921.

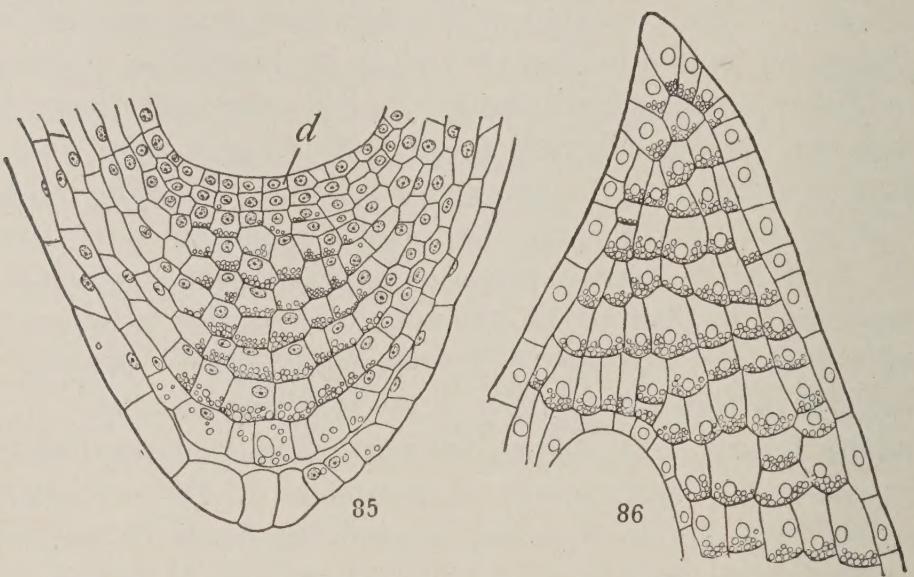
Newcombe, F. C. The supposed reversal of geotropic response. *New Phytol.* **22**: 281–288. 1923.

For other criticisms of the hydrion theory see *New Phytol.* **20**: 38–42, 246–247, and 247–248. 1921.

would settle upon a new and excitable side of the vacuole wall, starting into action the mechanism of the end response.

There are many objections to this form of the theory, which was suggested by the visible otocysts of Crustacea, and the appearance of the centrosomes, which were then supposed to be common in the cells of seed plants but which are now known not to occur prominently in plant cells.

In a more concrete form the theory has much to commend it, though it cannot yet be considered as firmly established. In this form no in-



FIGS. 85, 86. — Perceptive regions: 85, median longitudinal section of the root cap of *Roripa amphibia; d*, dermatogen; 86, apex of the coleoptile of the plumule of *Panicum miliaceum*. — After NÉMEC.

visible structures are predicated, but the principle is the same. Certain cells, notably those of the inner median portions of the root cap (fig. 85), the tip of the coleoptile in grasses (fig. 86), and a layer around the vascular cylinder in stems, contain rather large starch grains in such abundance as to attract attention. Moreover, these starch grains are freely movable, and in whatever position the organ rests, they accumulate on the physically lower side of the cells. They seemed to answer the requirement for bodies heavier than the fluid in which they lie, and therefore capable of setting up an excitation by coming to rest upon a part of the protoplast unaccustomed to their contact. It is assumed that certain areas of the protoplast are properly sensitive; that their excitation will start into activity the mechanism of curvature, which will eventually restore the organ to its normal position and so remove the irritating starch grains from excitable areas,

tumbling them again upon the side corresponding to the position of equilibrium.

These mobile grains are called *statoliths* and the cells containing them *statocysts*, after the analogy of the otocysts of the Crustacea, once thought to be organs of hearing, but now recognized as organs of equilibrium. The semicircular canals of the ear of vertebrates, with their fluid and mineral granules, have a similar function, giving the animal a sense of position or equilibrium.

Extensive anatomical studies have shown a remarkable parallelism between the presence of such grains and geotropic sensitiveness. Almost without exception, geotropic organs have mobile starch grains, while non-geotropic organs lack them. Moreover, when an organ, placed under unfavorable conditions (*e.g.* low temperature), has lost its mobile starch, it seems at the same time to have lost its geotropism, which is regained simultaneously with the rebuilding of the starch grains and not until then, although conditions favorable for response (had perception been possible) may have existed for much longer than the usual reaction time. This method of experimentation is, indeed, open to some objections; but the most serious one, namely, that the unfavorable temperature which determines the removal of the starch at the same time suppresses the geotropic irritability, is largely obviated by the fact that perception and the end reaction can be separately interfered with. Thus, by a temporary reduction of temperature, perception is not interfered with, for upon again raising the temperature with no further stimulation the end reaction proceeds as usual. Further, it is executed more promptly after the restoration of favorable temperature than it is when the low temperature is first used to eliminate the starch, and then at a favorable temperature stimulation is attempted. This indicates that the failure to obtain the curvature when there is no mobile starch is due to an interference with the mechanism of perception rather than with the mechanism of transmission or of growth.

The statolith theory of geoperception has a good deal of supporting evidence. Movable starch grains and ability to give the geotropic response occur together nearly everywhere in the plant kingdom. The rate of fall of starch grains is such that settling requires from a few to ten or fifteen minutes. Such periods of time are about right for the general presentation time for geotropic stimulation. The sine law for geotropic response is in agreement with theory. Shaking the starch grains gently as by tuning-fork vibrations is claimed to hasten settling of the grains, and also to shorten the presentation time.[1] Neverthe-

[1] Darwin, F. Statolith theory of geotropism. *Proc. Roy. Soc. London* B. **71**: 362–373. 1903. (Later on Bach claimed that shaking did not influence the reaction- and presentation-time.)

Bach, H. Über die Abhängigkeit der geotropischen Präsentations- und Reaktionszeit von verschiedenen Aussenbedingungen. *Jahrb. wiss. Bot.* **44**: 55–123. 1907.

less, proof of the correctness of the theory has not yet been possible. The main difficulty comes with the exceptions to the theory. In some cases geoperception and response occur without movement of starch grains. To account for such cases it is admitted that, after all, movement is not necessary, that gravity pulling on the starch grains in a different direction could stimulate the protoplasm to reaction. Again, it was noted in some cases that movable starch grains were present, but that no response occurred. The explanation here is that the protoplasm is not sensitive to the changed position of the starch grains.

If we make these admissions, however, we make the testing of the truth or falsity of the theory very difficult. That is approximately the status of the theory at the present time.[1]

The chemical theory of geotropism. — Whether statolithic starch is responsible for geoperception or not, it is certain that chemical changes are associated with the reaction of the stimulated organ. Studies of the chemical changes during response were first made nearly fifty years ago by Kraus.[2] Since that time Czapek[3] has studied the production and accumulation of homogentisic acid in stimulated organs, but his results could not be confirmed. Changes of water content of the tissues, probably turgor changes, occur, and Miss Schley[4] has reported changes in sugars, acids, and respiration in stimulated shoots of *Vicia faba*. The order in which she thinks these chemical changes occur is (1) increased respiration, (2) increased acidity, (3) increased turgor, and (4) increased production of hydrolyzable sugars at the expense of polysaccharides on the convex side of the stimulated organ. Phillips[5] was unable to correlate such chemical changes with the geotropic stimulus and response in the nodes of corn, but it is impossible for the plant to make the changed growth which it does make without some kind of chemical readjustment within its body.

Possibly the best theory of geotropic perception and response at

[1] Jost, L. Studien über Geotropismus. I. Die Verteilung der geotropischen Sensibilität in der Wurzelspitze. *Zeitschr. Bot.* **4**: 160–205. 1912. See also *Zeitschr. Bot.* **4**: 206–229. 1912.

[2] Kraus, Gregor. Über die Wasserverteilung in den Pflanzen. *Abh. Naturf. Ges.* Halle **15**: 49–120. 1880.

[3] Czapek, F. The anti-ferment reaction in tropiatic movements of plants. *Ann. Bot.* **19**: 361–457. 1906.

[4] *Loc. cit.* See reference 3, page 269.

[5] Phillips, T. G. Chemical and physical changes during geotropic response. *Bot. Gaz.* **69**: 168–178. 1920.

present is a combination of the statolith starch theory of perception, and some form of chemical theory of response.

The hydrion theory. — The most recent theory of geotropic response, and the least tenable, was proposed in 1920 by Small. He pictured the protoplasm of the stem tip as more alkaline than the isoelectric point of protoplasm because of the use of carbonic acid in photosynthesis in the green regions. The root region, however, because of accumulating carbonic acid in the absence of photosynthesis, was supposed to be more acid than the isoelectric point. When a protein is more alkaline than the isoelectric point, it ionizes in such a way that the protein ion bears a negative charge. That is, the protoplasm exists as calcium, potassium, and sodium proteinates in alkaline media, and the protein forms the anion in ionization. All anions are negative. But if the protein is more acid than the isoelectric point, it ionizes in such a manner that the protein ion bears a positive charge. In this case, when in acid media it acts like protein chloride, protein sulphate, or protein nitrate and forms the cation in ionization which is always positive.

Now, Small supposed that the colloidal protein ions would rise in the cell, like cream on milk, and give the cells of root and stem different electrical orientation. In the stems, the anions would rise and carry a negative charge toward the top of each cell. The lower parts of the cells would then be positive. By this process of "creaming" of protoplasm the cells would be polarized. The same thing would happen in the root, except that here the positive charge would rise to the top of each cell, and the lower part become negative. The polarized condition of the root would then be just opposite to that in the stem, positive above and negative below in each cell, instead of negative above and positive below, as was supposed for the stem.

Small supposed that, as a result of this difference, electrical currents would be set up in opposite directions in the two regions, an upward current in the stem region, and a downward current in the root region. When the current reached the periphery of the organ, it was supposed to flow laterally, in the direction of the axis of the stimulated plant. This horizontally flowing current, on the upper side of the stem and lower side of the root, was supposed to cause loss of semipermeability and consequently loss of turgor. This loss of turgor on one side of root and stem was thought to be the cause of the unequal growth that led to bending upward of the stem, and downward of the root. While

this theory shows ingenious reasoning, there is no evidence at all to support it.

Plagiotropic organs. — The erect position of certain organs is not necessarily determined by gravity alone, but may be due to the co-operative action of other stimuli. In like manner the oblique or horizontal position may be determined wholly by a response to gravity, or by some other single stimulus, or by simultaneously acting stimuli. Experiment alone can determine the agents in each case. Among plagiotropic organs which owe their position to gravity, some rhizomes that run horizontally beneath the surface of the ground are noteworthy. When such a rootstock is displaced by directing the tip obliquely upward or downward, curvatures ensue, precisely as in the case of parallelotropic roots, though, of course, the growth is much slower. This mode of reaction is known as *transverse geotropism* or *diageotropism*, corresponding to the positive and negative geotropism of parallelotropic organs. Quite similar behavior is to be seen in some peduncles, which are pendulous while the flower is in bud, but become in bloom horizontal, and in fruit erect. When the change of position can be shown to be due wholly to gravity, this indicates that the peduncle undergoes with age a change in its mode of response. Well-known examples are offered by the snowdrop and the wind flower. Less generally known are like changes in direction when certain stems, erect in the seedling stage, develop into horizontal rhizomes in an older stage.

Diageotropism. — Diageotropism of a somewhat modified type is seen in the branches of the primary roots of some plants. These grow out at a definite angle, and, if displaced, they will curve until the normal angle is again attained. Similarly the oblique branches of trees sometimes are decidedly geotropic, and even the pendent ones may show it. Only by the most cautious and precise experimentation in each case can it be ascertained whether the positions assumed are due to gravity. Unwarranted generalizations in this direction are particularly seductive. In far the greater number of cases the position of organs is determined by a complex of stimuli most difficult of analysis.

Twiners. — Among the most interesting of the complex phenomena are those exhibited by twining plants, in which geotropic reaction of a peculiar kind plays a most important part. Twiners have slender stems with a very long growing region, and a tardy development of the

lateral organs (leaves and branches), so that the long tips often look quite naked. These ends seem to travel in a spiral fashion around some suitable, slender support, and the mature plant is thus wound around it and clasps it tightly. At the outset the seedling, say of a morning glory, grows quite erect, and seems like a parallelotropic plant, as, indeed, a study of its reactions with a clinostat shows it to be at this period. After reaching a certain height the tip no longer grows erect, but declines to one side, and then a movement begins, quite like the irregular nutation that every erect plant makes, except that it is regular and more striking. The tip, standing in a nearly horizontal line, swings steadily around and is directed successively to every point of the compass. This may bring it into contact with a suitable support, around which it then proceeds to twine, the free tip continuing the swinging movement from the point of contact with the support. The fundamental feature of the twining, therefore, is the swinging motion.

Lateral geotropism. — Since the swinging movement does not continue when a twiner is properly rotated on a clinostat, it must be considered a response to gravity. As growth that can swing the tip sidewise can be effective only if it takes place on the flank, the inference is made that the stimulus, instead of finally affecting the side of the stem next the earth, as it does in the younger stages of development, now affects the flank, determining there more rapid growth. According as the right flank or the left grows faster, the tip will be swung like the hands of a clock or in the opposite direction. The twining may then be designated as clockwise or counter-clockwise. There is no fundamental reason, apparently, for one direction rather than the other. While usually the same species of plant twines always in the same fashion, closely allied species will differ in this; there are some species that twine indifferently in either direction; and there are a few in which the individual plant may change the direction of twining in the course of its development.

Rotation and revolution. — When growth of a given flank has swung the free tip around, this very act, by twisting the stem on its own axis, brings a new segment of the stem into the flank position and so exposes it to excitation.

This may be understood by representing the stem by a hexagonal pencil. If the side on which the name is stamped face the right with the pencil horizontal and the point away from the body, then this right flank may be imag-

ined to be the one whose growth is accelerated; by that the point would be swung to the left, and by the time it has passed over 90° the pencil would be rotated on its axis through 90°, so that the stamped side would now face upward and the angle that was first at the bottom would now be the flank. This rotation may be imitated, if it cannot be seen to be a mechanical necessity when a horizontal portion of an erect stem is so rotated, by sticking the end of a pencil into a piece of rubber tubing just stiff enough to bend into a quadrant under its weight. Now upon swinging this apparatus without torsion, as can be done by holding the end of the tube and pushing the test pencil around with another, the rotation will become at once evident, being complete when one revolution is completed.

The new flank thus brought under the influence of gravity has its rate of growth increased, which swings the tip further, rotates the free part of the axis, and so brings another segment into the flank position. Given the sensitiveness of the flank to gravity, the revolving movement follows as a necessity.

The support. — When a stem is swinging thus, if it come into contact with some obstacle near the tip, flexure may carry it past the object; but if it strikes the obstruction further back, the bending may not be sufficient to carry the axis past the obstacle, particularly if it be of moderate size. Instead, curvature will soon occur in the part projecting beyond it, and the revolving movement will be continued by the apical portion, which steadily wraps itself around the support. In the nature of the case it is not possible for twiners to wrap about large supports, nor those that are too nearly horizontal. Plants differ much in their capacity in these two points, a difference which depends chiefly upon the relative length of the growing portion of their stems, and consequently upon the precise distance of the most actively growing region from the apex. Few twiners encircle supports more than 15 cm. in diameter, or those that lie nearer the level than 45°.

Straightening. — The coils that a twiner forms at first are loose and of low inclination. Later they become steeper and hug the support tightly. This seems to be due to a return, in the last stages of growth, to the apogeotropism that they possessed in the seedling period, so that the stem starts to erect itself, with the effect stated. Very commonly the surface of the stem is rough, being ridged or angled or furnished with stiff hairs, which prevents slipping from a support too easily or sliding along it. Inspection of the stem in the regions no longer growing shows that it is twisted, the longitudinal ridges coursing spirally around the axis in a direction the reverse of the twining. This torsion

is mainly the result of the final erection of the stem, though other causes coöperate to increase or diminish it.

This also is a mechanical necessity of the behavior. It can be imitated by coiling a long piece of rubber tubing on a table, marking a crayon line along the upper surface, and then lifting the inner end of the coil while the other end is held on the table, both ends being prevented from twisting in the fingers. Then it will be seen that the line apparently passes spirally around the tube. because the latter is twisted by the steepening of its coils.

The tardy development of the leaves and branches is very evidently an advantage in twining, for they would greatly impede the revolving movement and the subsequent tightening of the coils. When the branches do develop, they show the same behavior as the main axis.

This explanation of twining is not wholly satisfactory, because there are details of the process, and some features that appear only under experiment, that are not clearly accounted for; but it is far the best of the many theories that have been proposed, and in the major outlines that have been presented here it is certainly correct.

(2) Thigmotropism

Tendrils. — Many plants are sensitive to mechanical stimuli such as contact or friction, as shown by the alterations of the rate of growth that lead to curvature. This phenomenon is *thigmotropism.* The tendrils of climbing plants exhibit the most remarkable sensitiveness to mechanical stimuli, and it is by this means that their attachment to supports is secured. Tendrils are slender, even threadlike, lateral organs, branched or not, sometimes occupying the usual place of a branch, sometimes that of a leaf or of one or more leaflets of a compound leaf. They are therefore formed successively with the development of the main axis and its chief branches, so that the plant is constantly laying hold of a support by younger and younger tendrils. It may thus climb to great heights, while the main axes remain very slender and wholly unable to support their own weight, much less that of foliage, flowers, and fruit. The most important feature of the tendril is its irritability to contact, and the curvatures which follow as end reactions.

Behavior. — When a tendril is young and only about one fourth grown, it may be either straight or curled up into a loose spiral, of which the convex surface corresponds to the under side. If coiled, it unrolls as its period of rapid growth begins, at which time also begin

nutating movements that are almost as regular as the revolving movements just described in the twiners. These tendril movements, however, are not due to any known external stimulus, but must be called at present autonomic. The tip is thereby swung in all directions and is thus likely to come into contact with some suitable support. When it does so, it quickly wraps around it. After a time, through continued and unequal growth in length, spiral coils appear in the region between the axis and the attached part, increase in number and closeness, and become more and more firm, until this part has become a veritable spiral spring by which the plant is slung to its support. These results are attained in the following way:

Stimulus: friction. — The tendril is sensitive to contact usually throughout its whole length, and on all sides, but most so towards the tip. Yet it is not sensitive to contact in the narrow sense; it is because things come into contact with the tendril in more than one place when they touch, so that it is only by multiple and successive contacts, and usually by shifting contact or friction, that the tendril is excited. Liquids (even the heaviest, mercury), if entirely free from solid particles, and perfectly smooth solids, like gelatin, do not produce excitation. Rain, therefore, does not cause useless movements of tendrils. But very slight rubbing movements of excessively light objects suffice to start them. It has been found, for example, that a bit of thread, weighing by estimate only 0.00025 mg., if moved by the wind over a very sensitive tendril, will induce curvature.

While the tendril may be sensitive throughout, the responses evoked by excitation differ sometimes according to the region stimulated. Thus, a stimulus applied to the " under " side, which at the time of greatest sensitiveness has usually grown near the apex a little less than the other, so that at the tip it is slightly concave, results in a curvature. So also does stimulation of the flanks, and in some tendrils that of the upper side too. But there are some others which give no sign if rubbed on the upper side, except that stimulation there will inhibit a simultaneous stimulation on the under side, which ordinarily would result in a curvature.

Primary response. — The first result of slight rubbing contact with a suitable support (that is, one that is small enough for the tendril to encircle, no matter in what position it stands) is a prompt curvature. In sensitive tendrils under favorable conditions this follows in the course of a few seconds (5–30), but in others in a few minutes. The

facts observed are that the cells on the convex side become suddenly considerably elongated, while those on the concave side become somewhat shortened. This and the promptness of the end reaction suggest a turgor change, and many observers have concluded that such is the mechanism of the primary curvature, and that it becomes fixed later by growth. Others attribute these results to a very rapid and extraordinarily sudden growth of the cells of the convex side, and to the consequent compression of those on the concave side. It is not improbable that the truth in this, as in many similar recondite and much controverted matters, will prove to lie between the contentions. So it may very well be that a turgor variation begins the movement, whereupon growth follows it up more promptly than usual, and extends and completes the encircling of the support.

Secondary response. — After the tendril has become firmly attached, the excitation extends toward the base of the tendril, producing an inequality of growth on the opposite sides (in this case the " upper " side becomes the convex one) that throws this part of the tendril into coils.

This coiling may be rudely but essentially imitated by placing in a pan of water a narrow strip, slit from the scape of a fruiting dandelion which has not attained its full height, and by pinching each end in a short folded piece of sheet lead to prevent twisting. After a few hours the strip will be found coiled into a spiral, with one or more reversals of direction just as in the tendril, though more irregularly. Here the tissue next the pith cavity grows and becomes more turgid than the epidermal and cortical tissues. The reversal of coil is a mechanical necessity if the ends are not free to rotate.

These coils are not merely the result of continued growth of the tendril; for if one not full grown becomes attached, it does not reach its possible maximum length, but from that time grows only in such a way as to throw it into the spiral coils. One which does not become attached grows longer and longer, but finally shrivels, usually without coiling. Sooner or later, upon the cessation of this second phase of growth, the phase of maturation is marked by the development of mechanical tissues, which add strength to the elastic coils. The nature of the stimulus that brings about the final coiling is uncertain. It may be the strain from the weight of the plant after becoming fastened, or the spreading stimulation from the contact pressure (for the attachment coils compress the support), or some unsuspected stimulus may be brought into action. There are many other stimuli which will evoke

reactions from the tendrils, but none which in nature has any importance.

Sensitive petioles. — There are other plant organs that behave in a similar way to the tendrils, though none of them is so sensitive. The petioles of *Clematis* and of the climbing *Tropaeolum*, or "nasturtium," are familiar examples. While such petioles do not wrap themselves around the support nor form spiral coils as well as a tendril does, nevertheless they are efficient prehensile organs, enabling the plants to climb high.

Dodders. — Any account of twining and climbing plants would be incomplete without mention of the dodders (*Cuscuta*), leafless yellowish parasites that wind their stems around and clamber over erect herbaceous plants, sending haustoria into their stems, whence they obtain food and water. In the first stages of development, the species that have been studied germinate in the soil, and the young seedling behaves as a twiner; but shortly after it has found a suitable host and begun to twine around it, the lower part of the stem dies away, while the upper part continues its growth at the expense of the host. The further twining, however, instead of being dependent upon gravity, is the result of a contact stimulus like that which enables tendrils to secure a hold, so that the parasite enwraps supports in all sorts of positions. In the possession of these two modes of response at different periods of development, the dodders are unique.

(3) Traumatropism

The wounding of plants produces immediate reactions, mostly invisible, but root tips may be so wounded as to lead to curvature. If an active tip be branded on one side with a hot iron or glass rod, or if it be similarly cut or otherwise injured, the tip will turn to one side. When the injury is severe, this may so seriously impair the tissues on the injured side that their growth will cease, and the injured side will become concave near the point of injury, because there the tissues shrivel and the growth of the other side goes on. This is not a true reaction, since the result is due merely to mechanical interference with growth. On the other hand, if the injury is one that does not deeply involve the tissues of the injured side, a curvature will follow that turns the tip away from the injury. Here an excitation started by the wound has spread thence to the region of most rapid growth, inducing a true tropic curvature. After experiments by attaching bits of cinder, paper, and the like to root tips by means of gum, it was believed that the root tip, by its sensitiveness to contact, was a sort of directive organ, which could feel its way through the soil, and avoid injury. But in these experiments the gum injured the cells, and it, not the attached particle, was the stimulating agent, so that the response was actually to injury and not to contact. It is not probable that sensi-

tiveness to injury is of any advantage to the plant, as it undoubtedly is to a conscious organism. Occasionally, of course, traumatropism might be advantageous to a plant in getting a root tip once injured out of immediate danger of further injury.

(4) Rheotropism

Roots grown in a current of water of adequate velocity may respond by directing their tips against the current. In this case the stimulus might be the strains set up by the pressure of the current, or the impact and friction of the water particles against the surface. Its precise nature is not satisfactorily determined, but it seems to be the pressure of the water and the resulting strains rather than mere contact or impact. The whole of the growing region seems to be sensitive, and not the tip alone. It is not apparent that this reaction can have any significance for the plant in nature.

(5) Chemotropism

Of fungi. — Chemical compounds may not only be usable in repair and constructive work, but may so affect the living substance and its metabolism as to act upon it as stimuli. Since by diffusion such chemicals may act from one side, these stimuli may be directive, causing curvatures toward or away from the source, which are manifestations of chemotropism. Very striking reactions to chemical compounds of many sorts have been ascribed to the hyphae of fungi and to pollen tubes. Chemotropism of the latter may be maintained still, as it has not been seriously impeached; but that of fungus hyphae has been brought under suspicion by certain investigation, and may be either established or disproved by further study. For the hyphae to be sensitive, especially to carbohydrate and other foods, would be of much service in inducing them to grow in directions that would bring them into favorable feeding regions, and precisely this power has been ascribed to them. For instance, when certain fungus spores are sown in a layer of gelatin containing no nutritive materials, between layers of gelatin, on the one side with nutritive material and on the other side without, it is reported that the hyphae turn toward the layer of nutritive gelatin. The same reaction was found to occur when the central layer contained food provided the outer layer had enough more of the same to act as a stimulus. (In this case the ratio had to be about 10 : 1. See Weber's law, p. 252.) Likewise the hyphae grew through fine perforations in thin plates of mica or celluloid, when the nutritive gelatin was thus separated from the other, suggesting the way in which fungus hyphae, arising from spores on a leaf, turn into a stoma and so find their way into the interior of a leaf of their host. In fact, when

leaves are injected with a solution of food, like sugar, fungus hyphae of many kinds are reported to turn into the stomata, though they do not naturally grow on the leaves used. A great variety of substances were tested in similar ways. Some proved to be attractive, some repellent; and the reaction varied according to the concentration of the solute, though generally the hyphae were injured before the limits of concentration for repelling effects had been reached.

On the other hand, an apparently careful repetition of many of these experiments gave negative results, in that the number of hyphae reacting positively is so slightly in excess of the number indifferent or negative, that the results seem scarcely more than chance, or ascribable to other than the cause assigned heretofore. A complete restudy of the matter will be necessary.

Of pollen tubes. — When pollen tubes are developed under a cover glass in company with a bit of the stigma of the same plant, they turn toward it, from whatever direction they first issue. An ovule or a bit of the wall of the ovary is likewise attractive. Investigation shows that soluble carbohydrates and proteins are here the attractive substances. It seems likely, therefore, that the growth of the pollen tube toward the ovules is directed by the diffusion of such substances, which are always found in these organs. (See the chemotaxy of sperms, p. 252.)

Arëotropism. — A special form of chemotropism has been called *aërotropism* and was first ascribed to roots. When certain gases, especially oxygen, diffuse against young roots from one side, it is reported that the root curves toward the source of the gas. These results also have fallen under suspicion. Recent investigations are conflicting; and one is left in some doubt whether to ascribe the curvatures to a true reaction to gases, in accordance with the weight of evidence, or to moisture, in which case they belong to the following special category of chemotropic response, hydrotropism.

Stems also have shown sensitiveness to O_2 and CO_2, and it may be that aërotropism is more general than has heretofore appeared. It is not evident that it can be of any great advantage to either roots or stems, except, perhaps, those of swamp plants.

Hydrotropism. — Another special form of chemotropism, which has been named hydrotropism, designates the sensitiveness of roots, the hyphae of some fungi, the rhizoids of liverworts, etc., exhibited by turning toward or away from the source of diffusing water vapor, or capillary water in soils. When seedlings are grown in an atmosphere less than saturated with water vapor, so that the roots, as they grow,

pass further and further away from a wet surface,[1] it will be found that they deviate presently from the perpendicular, inclining toward the wet surface; soon again they turn downwards, but once more return to the moisture, and this may be repeated many times. Plainly the roots are subject here to two stimuli acting nearly at right angles, gravity and the diffusing vapor. First the one dominates and then the other. Were it not for the long reaction times the root might be expected to take an intermediate direction, the resultant of the effects of the two stimuli; but as in the case of geotropism alone (see p. 264), the after-effects carry the root tip past the position of equilibrium, whereupon the other stimulus gives it such strong and long excitation that its after-effects carry the root again past the equilibrium point; then the gravity stimulus comes upon it again; and so it weaves back and forth.

The vegetative hyphae of the mold fungi may show positive hydrotropism and their sporangiophores negative hydrotropism. It can easily be shown that the rhizoids of *Marchantia*, which normally grow straight downward, will deviate toward a moist surface in the same way as roots; only the moisture stimulus is dominant over gravity. Roots in the soils also grow towards the moister regions, and especially do they tend toward tile drains, into which they may penetrate, often branching profusely enough to plug up the drain completely. Part of this directive effect may be due, and probably most of the branching is due,[2] to chemical stimulation by the solutes.

(6) Phototropism

Stimulus. — Of all the external conditions that act upon plants, light is one of the most variable, for from time to time it differs in direction, in intensity, and in quality. Quite apart from its fundamental relation to all life in furnishing the energy for food making, are its effects as a stimulus. Whereas the most effective quality of light for food making is the red-yellow, the most effective light as a stimulus is that near the violet end of the spectrum, from 400 μ to 500 μ, with the maximum stimulation at 460–470 μ. Since this is the region of least energy, the shortness and frequency of the waves are the important features of light as a stimulus. In this respect the red end of the spectrum, though its energy is far greater, behaves as darkness.

[1] As by planting them in coarse sawdust held in place on the under surface of an inclined board by bobbinet.

[2] In which case this is a morphogenic effect. See p. 214.

Response. — In general the response of plants to light differs according to the usual attitude of the organ and its mode of growth, for which indeed light is largely determinative. Parallelotropic organs respond by directing their tips toward or away from the source of light, while plagiotropic organs place themselves more or less at right angles to the direction of the rays. Primary stems, therefore, are mostly positively phototropic, and some roots, particularly aërial roots, are negatively phototropic; while leaves are mostly transversely phototropic or diaphototropic.

These phenomena were first known as heliotropism, etc., and are often still so called, because the sun in nature is the source of all light. It seems better, however, to use the wider term, since plants respond in the same way to artificial light, which is so largely used in experimental work. The general result of these reactions is the same as of those to gravity, so far as the same organs are sensitive to both stimuli, though the two act from opposite directions in nature.

Intensity. — The intensity of the light may determine either a positive or a negative curvature, and within certain limits between these two there is a range of intensity which calls forth no visible reaction; this is the point of phototropic indifference. It is by no means the point of no excitation. At high intensities (over 13,600 M.C.S.)[1] that call forth negative curvature, injury soon appears. Near the lower limit of intensity that can produce an end reaction, plants show themselves very sensitive to light. Thus, radish seedlings respond to the light of a single candle at a distance of about 8 m., the broad bean (*Vicia faba*) at 22 m., and a cress (*Lepidium sativum*) at about 55 m. The differences that plants can distinguish are within the limits of error for the unaided eye, and are not very easily distinguishable even with the photometer.

Time relations. — The presentation time or threshold stimulus, of course, depends upon the intensity of light used, and is approximately inversely proportional to it. The greatest range of presentation time recorded is that for etiolated seedlings of oats, being 0.001 second with light intensity of 26,520 Hefner candles, and 43 hours with light intensity of 0.00017 Hefner candle. Intermediate light intensities give corresponding inverse proportional intermediate presentation times. The product of the intensity multiplied by the duration ($i \times t$) is approximately a constant, as is shown in the following table:

[1] The meter-candle-second, a standard unit of light intensity.

Intensity in Meter Candles	Duration in Seconds	Quantity of Stimulus ($I \times t$)
0.00017	154800.0	26.28
0.00085	21600.0	18.36
0.00477	3600.0	17.17
0.0898	240.0	21.55
5.456	4.0	21.82
1902.0	0.01	19.02
26500.0	0.001	26.50

These figures from Blaauw,[1] however, which average 21.5 M.C.S. give a rather high value for the quantity of stimulus required for the response of *Avena*. Noack[2] found 12 M.C.S., and Guttenberg[3] 2.3. M.C.S. for the same plant. The fact that a definite quantity of stimulus is required to produce a response has been called the *quantity of stimulus law*. With different sources of light, different varieties of *Avena*, and different laboratory conditions, the threshold quantity of stimulus varies, and such differences may account for the variations found by Noack, Blaauw, and Guttenberg. As a rule the younger an organ is, the more sensitive it is; but this is by no means universally true. The reaction time varies from a few minutes to some hours, depending upon the temperature, the intensity of the light, and the general condition of the plant.

Reversal. — The reactions to light also are often reversed with age. This is especially seen in flower stalks, which at the time of blooming are likely to be positively phototropic, but later, during the ripening of the fruit, many become negatively phototropic, carrying the fruit under the leaves or even into crevices of the soil or rocks on which the species grows.

Mechanism. — The mechanism of the response is the same as in geotropism, and occurs in the same region; namely, that of most active growth, where one side grows more rapidly than the other, leading to a curvature whose tendency is to direct the axis into the line of the light rays. This inequality of growth is brought about by its acceleration on the convex side and by simultaneous retardation on the concave side.

[1] Blaauw, A. H. Die Perzeption des Lichtes. *Rec. Trav. Bot. Néerl.* **5** : 209–372. 1909.

[2] Noack, Konrad. Die Bedeutung der schiefen Lichtrichtung für die Helioperzeption parallelotroper Organe. *Zeitschr. Bot.* **6** : 1–79. 1914.

[3] Guttenberg, H. von. Studien über den Phototropismus der Pflanzen. *Beitr. allg. Bot.* **2** : 239–247. 1922.

These changes in rate are not due to the fact that the rate of growth is retarded by light (see p. 225), for this (apparently applicable to positive phototropism and once an accepted explanation) could not account for the acceleration on the convex side, nor for any of the changes in negative phototropism. The reaction is determined by the mechanism of the parts concerned and not by the *direct* influence of the stimulus.

Perceptive region. — In many phototropic reactions there is a distinct perceptive region, a propagation of the excitation, and an end reaction in a different region. Thus when seedlings of millet raised in the dark are exposed to lateral illumination, the sharp curvature that presently appears in the axis (" hypocotyl "), which is rapidly growing, can be shown by appropriate shading to owe its origin to the stimulus perceived by the leaf at the tip (" cotyledon ") and not to excitation of the axis itself. In a similar way the seedlings of oats show that though the whole of the subaërial part is sensitive to light, the tip is much the most so, and that excitation, spreading thence downward, dominates even contrary excitation set up in the lower parts.

Transmission of excitation. — Since perception occurs mainly in the " cotyledon " of *Setaria*, and in the tip region of the coleoptile of *Avena*, whereas the curvature occurs much farther down in the responding organ, there must be a transmission of excitation from the tip to the place of response. The transmission is more rapid from above downward than from below upward. Since cutting the vascular bundles does not stop the transmission of excitation, it is probable that the living cells of the parenchyma regions (cortex) are involved in the propagation of the stimulus. The plasmodesmen and the circulation of protoplasm may share in producing this phenomenon.

Careful experiments by Paál,[1] and by Stark,[2] and Drechsel[3] indicate that some substance is formed in the perceptive region that is carried to the responding region. A stimulated tip of *Avena* coleoptile could be cut off before response occurred, and then cemented back on to the decapitated coleoptile with gelatin. The excitation passed right through the gelatin, which shows that the stimulus can pass across a gap of non-living material. If plates of mica or tinfoil are used to

[1] Paál, A. Über phototropischen Reizleitung. *Jahrb. wiss. Bot.* **58**: 406–458. 1918.

[2] Stark, P. Studien über traumatotrope und haptotrope Reizleitungsvorgänge mit besonderer Berücksichtigung der Reizübertragung auf fremde Arten und Gattungen. *Jahrb. wiss. Bot.* **60**: 67–134. 1921.

[3] Stark, P., and Drechsel, Otto. Phototropische Reizleitungsvorgänge bei Unterbrechung des organischen Zusammenhangs. *Jahrb. wiss. Bot.* **61**: 339–371. 1922.

separate the stimulated tip from the responding organ, there is no response. The excitation, then, cannot pass an impermeable barrier. The gap must either be permeable to some substance, or capable of transmitting some kind of change that induces response in the lower parts of the coleoptile.

The existence of growth hormones in the coleoptiles of *Avena* has been demonstrated by the brilliant work done in the Laboratory at Utrecht under the direction of F.A.F.C. Went.

The most recent contributions are those of Söding, H. Zur Kenntnis der Wuchshormons in der Hafercoleoptile. *Jahrb. wiss. Bot.* **58**: 587–603. 1925; Dolk, H. E. Concerning the sensibility of decapitated coleoptiles of *Avena sativa* for light and gravitation. *Proc. Kon. Akad. Wetensch.* Amsterdam. **29**: 1113–1117. 1926.

Went, F. W. On growth-accelerating substances in the Coleoptiles of *Avena sativa*. *Proc. Kon. Akad.* Amsterdam. **30**: 1926; and Went, F. W. Wuchsstoff und Wachstum. Dissertation. Utrecht. 1927. The last paper puts the existence of growth hormones in *Avena* beyond reasonable doubt.

Stimulated tips could be cut off and transplanted to unstimulated coleoptiles, but still cause a response in the basal region of a coleoptile that had not been stimulated. They even found it possible to transplant a stimulated tip of one species of grain to the unstimulated coleoptile of another species of cereal and obtain a response. Often the response was weak in such cases, but the basal portion of a barley coleoptile was found to respond better with a tip from *Avena* than with a transplanted barley tip.

It was also shown that pieces of gelatin through which the stimulus has passed are capable of calling forth a reaction in an unstimulated coleoptile if the latter is decapitated and a piece of the gelatin is placed in contact with the upper end of the decapitated organ. The direction of curvature could be controlled by careful placing of the small pieces of gelatin on one side or the other of the middle of the coleoptile.

The results suggest the production of a phototropic substance of some kind, similar to the hormones which are thought to be related to the problems of correlation, wound responses, etc. The method of transmission of this substance, if we really have a substance formed, is not clear. The rate of transmission exceeds that of diffusion, and may involve protoplasmic streaming, or some other protoplasmic mode of progression of excitation.

What is perceived? — Nothing is known as to the mode of perception or the structure of the perceptive organ. Indeed, it is not entirely

certain what sort of stimulus the plants perceive; whether it is the direction of the rays, that is, the line of propagation of the waves, or whether it is inequality of the illumination of different sides. It has even been suggested, in casting about for something tangible, that plants distinguish between the different pressures in the lighted and shaded portions.

It has been shown that the impact of the ether waves of full sunlight produces a pressure equal to about half a milligram per square meter. In a seedling of oats at this rate the plant would have to be sensitive to a difference of five millionths of a milligram and probably to one tenth of this infinitesimal amount. This is simply inconceivable!

It seems most likely that it is the difference in the lighting that is perceived, for the intensity of the stimulus has an important bearing on the form of the reaction, and plants are able to respond to differences of illumination coming from different sides that are too small for the eye to distinguish. The weight of evidence brought forward in recent years is favorable to the theory that the plant perceives a difference in intensity rather than a difference in direction. The careful experiments of Guttenberg,[1] Buder,[2] and Nienberg,[3] have brought forward convincing evidence in favor of the light intensity theory, although there are still workers who believe that light direction exercises the major influence in response.

Plagiotropic organs. — The behavior of plagiotropic organs toward light is especially interesting, because it seems to be usually of the very greatest importance for the welfare of the plant in food making by leaves, thalli, etc. The fact that the leaves of most common plants, set before a window, place themselves at right angles to the incident light, attracts attention at once. If the pots be turned around, the position of the leaf blades will soon be changed, and they face the window

[1] Guttenberg, Herman Von. Untersuchungen über den Phototropismus der Pflanzen. II. Neue Versuche zur Frage nach der Art der Lichtperzeption. *Ber. d. bot. Ges.* **37**: 304–310. 1919.

[2] Buder, J. Zur Kenntnis der phototaktischen Richtungsbewegungen. *Jahrb. wiss. Bot.* **58**: 105–120. 1917.

Neue phototropische Fundamentalversuche. *Ber. d. bot. Ges.* **38**: 10–20. 1920.

[3] Nienberg, W. Die Keimungsrichtung von Fucus-Eiern und die Theorie der Licht Perzeption. *Ber. d. Bot. Ges.* **40**: 38–40. 1922.

Die Polarization der Fucus-Eier durch das Licht. *Wiss. Meeresunters.* Abt. Helgoland (Festschrift für Friederich Heineke) **15**: Heft. 1. Art. 7. pp. 1–11. 1923.

Die Wirkung des Lichts auf die Keimung der Equisetumspore. *Ber. d. bot. Ges.* **42**: 95–99. 1924.

again. Thus the leaves obviously come into a position most advantageous for receiving the maximum of energy for photosynthesis. The corresponding orientation in the open shows that it is not the direct sunlight alone to which the leaves respond, but rather what may be distinguished as sky light; that is, the brightest diffused or reflected light. Indeed, in some cases the direct sunlight is evidently too intense, and the plane of the blades is set at an angle to the direct light, the edge in some plants being directed upward.

Compass plants. — When the position of leaves is uniform or nearly so, and corresponds approximately with the plane of the principal meridian, the plants are known as compass plants. The wild lettuce, *Latuca Scariola*, is the most widely distributed of these, and on the prairies and along railways, the compass plant *Silphium laciniatum*, which illustrates the habit far better, is common. Other plants in this and other countries have the same habit. That this is a response to intense light is seen easily in the lettuce, for when this plant grows in the shade, its meridional position is not assumed.

Fixed light position. — The reaction of a leaf to light can occur only while it (especially the petiole, which is the seat of most curvatures) is still growing or capable of growing. During this period the habitual responses lead finally to a position known as the fixed light position, a sort of resultant, which on the whole gives the blade the most advantageous illumination. One result of this is the arrangement of blades in such a way as to avoid shading one another. This produces the so-called leaf mosaics. The movements of the leaf in attaining these positions may involve curvature, lengthening, and twisting of the petiole and even of the blade itself.

Perceptive region of leaves. — Perception in most cases seems to occur in the leaf blade, whence the excitation is propagated to the petiole, whose upper parts grow for the longest time, and even after elongation has ceased may be started into growth again by the light. In some cases, however, the petiole itself may be sensitive to light, and may either cooperate with the blade, or alone be responsible for both perception and curvature.

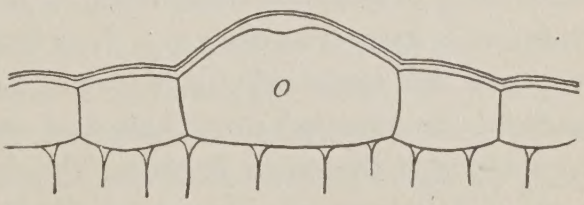


FIG. 87. — Ordinary epidermis and "ocella" (*o*) of leaf of *Dioscorea*. — After HABERLANDT.

The mechanism of perception has been sought in the epidermis of the blades. It has been found in some cases that the epidermal cells are domed and that they act as lenses (fig. 87), focusing

the light upon the lower side of the cell, so that a spot in the center is much more brightly illuminated when the light strikes at right angles. The position of this area is shifted when the leaf blade is oblique to the rays. Correspondingly, it is assumed that the protoplast is excited when the bright spot rests on any but the central area. There is no doubt that the structures described concentrate the light, for that can be shown photographically; but there are sensitive blades in which domed epidermal cells are wanting, and experiments do not yet unequivocally sustain the assumed distribution of irritability. The perceptive organs of leaves have not been located other than by this still doubtful hypothesis.

(7) Other tropisms with radiant energy

Electrotropism. — Currents of electricity passing through the medium in which plants are growing, and presumably through the organs themselves, evoke various curvatures according to the density of the currents used. By nature roots lend themselves especially well to experiment. Some of these responses, and possibly all of them, are due to one-sided injury of the roots. The effects appear to be due to electrolysis of the solutions used; but whether by the direct action of the ions outside or by the withdrawal of ions from the protoplast is not certain. Electrotropism or galvanotropism may therefore be hardly more than a special form of chemotropism. It does not seem likely that such stimuli act to any important extent in nature. The more important effects of galvanic and static currents upon development have already been described (see p. 230).

8. THE DEATH OF PLANTS

The cycle ends. — From the foregoing it has become evident that the growth and development of plants does not proceed uniformly, but that it is profoundly influenced — one may even say controlled — by external conditions; and since many of these external conditions evince a decided periodicity, growth and development exhibit a corresponding periodicity. But it has also become apparent that growth and development are likewise affected, and in many particulars as profoundly affected or controlled, by factors that are wholly internal, so far as is known at present. It is found, further, that these factors may give rise to periodicity in growth and development; for, however uniform the external conditions may be, neither proceeds uniformly. In nothing is this more impressively shown than in the fact that the cycle of development, in spite of all that can be done, sooner or later comes to an end, and the plant perishes, leaving behind comparatively few living cells, if indeed it leaves any, out of the unnumbered millions that may have constituted its body.

No inherent reason for death. — There does not seem to be any inherent reason why a plant should die. The material of which it is composed is all the while undergoing decomposition and repair. In a perennial plant, like a tree, the tissues in great part are renewed annually, so that though the living and the dead stand together as a sort of unity, which may have occupied the place for centuries, the oldest of the living parts may not be more than one or two centuries old. In such a plant, however, it becomes increasingly difficult to supply the extremities with the needful materials, because they are steadily becoming separated by greater and greater distances. The leaves are yearly further from the ports of entry for water, and the roots are yearly further from the source of food. With expanse of branching, mechanical overthrow threatens more and more. Thus the physical conditions are steadily becoming more severe, and it is easy to imagine why the plant must finally succumb. Yet the long persistence, even after it has become evident that a tree has reached the practical limit of growth, shows that there is nothing in the living parts themselves which determines the end; and still more is this shown by the fact that cuttings may be taken from an old tree and successfully started upon a new cycle which may be as long as the parent's. Thus, the Washington elm at Cambridge struggled against adversity for nearly half of a century, until it finally succumbed in a losing fight; but a cutting from it is now a thrifty, well-grown tree on the Boston Common.

Reproduction. — In the smaller plants the inception of unfavorable conditions is often a signal for the gathering together of all the living material into a form that can endure adversity, as with the encystment in bacteria, fungi, and algae. Under these circumstances also the protoplasm is divided into several or many parts, each appropriately protected; thus multiplication becomes possible if more than one part escapes injury and finds suitable conditions again for development (see *Botrydium*, p. 34, and many other illustrations in vol. I, *Morphology*). This simple situation has been worked out, in the higher plants, into elaborate mechanisms of reproduction, which are now not always obviously related to the inception of unfavorable conditions. Yet methods of cultivation indicate that the formation of spores, even in the seed plants, in which naturally it often far precedes the period of flowering, may be initiated by conditions unfavorable for vegetative growth. Until these conditions can be more exactly designated and analyzed, it is unprofitable to consider them more in detail. At

present, then, all that can be said is that unfavorable conditions bring about a redistribution of the living material, of which as much as possible resists and persists. Thus, since the beginning of things, we assume, there has been an unbroken chain of living matter, shaping itself for a time into organisms more or less complex, and then retiring into the simplest and least exposed forms, to begin another cycle of development when the conjunction of internal and external forces permitted.

What is death? — The abandonment by the living protoplasm of a body previously constructed, or the destruction of the protoplasm wholly or in great part, is what is usually meant by the death of a plant. Since plants conspicuously lack individuality whenever they become more complex than a single cell, the severance of a plant, even the highest, into two or more parts may not bring death, as it does to so many of the higher animals, but rather renewed vigor. Correspondingly, the death of even a large part of the body does not necessarily bring death to the whole, but often likewise renewed vigor to the parts that persist.

Local and general death. — Extensive local death, as this may be called for convenience, is possible in plants without the serious consequences that follow in the higher animals, first because plants have so little specialization of organs and so many of the same kind; second, because they have no circulatory system that might rapidly distribute to other parts deleterious substances arising in the dead region, and so cause their injury or death; and third, because they have no nervous system, putting into quick communication sound distant organs with hurtful stimuli from the dead ones. Yet these differences, on the surface so marked, are in reality not fundamental, for what is general death in the animal is in reality only an extension of local death to the several tissues and organs more rapidly than in plants. But each part dies at its own rate and only because the interruption of the activity of one organ has created conditions unfavorable to the other.

Irreversible reaction. — The phenomena of death are not easily described. Certain changes in the appearance of the cytoplasm are visible under the microscope (such as are familiar in fixed cells and are too commonly thought of as the normal appearance of cytoplasm), chiefly aggregation and vacuolation; but the significance of these is not known. Alteration in the chemical processes and different behavior, especially permanent insensitiveness to external stimuli, are

the most important marks of death. During life the protoplasm is constantly adjusting itself to new conditions, each response suited to the stimulus, whether in a favorable or unfavorable direction. These responses of normal life are assumed to be reversible, as are many chemical reactions. But when the responses to severe stimuli become irreversible in too great measure, the possibility of readjustment to new stimuli is past; this condition is death.

During life, the physical and chemical reactions which constitute living run along in coördinated fashion. Many of these reactions depend upon one another in turn. Such reactions are said to be concatenated, or coupled, reactions. Usually in these cases the end products of one reaction form the starting point of another, and a whole chain of reactions occur in a series.

The enzyme catalysts which are involved in these reactions perform their functions in an orderly way, probably because the colloidal organization of the protoplasm during life keeps the enzymes localized where their functions are to be performed. Each colloidal entity may be the scene of reactions that other near-by catalysts are unable to disturb because the colloidal structure holds them apart.

One of the processes accompanying or preceding death is a change in the permeability of the protoplasm. The colloidal structures lose their power to hold the catalysts apart for their separate functions. The enzymes pass through the limiting surfaces, and seem to diffuse more generally through the protoplasm. As a result of this breakdown of enzyme control, autolytic changes begin, and coördinated activity passes over into uncoördinated breakdown. The changes in permeability which precede death have been shown by Osterhout[1] to be reversible if they do not go too far, and recovery is possible. But if the changes go too far, they become irreversible, or at least irreparable, and death follows as the uncoördinated enzyme actions and fermentations become general throughout the affected tissues of the plant.

Diseases. — Plants are often killed by diseases which may arise from the disturbance of function wrought by external agents, such as the elements of climate, the solutes of the soil, gases in the air, etc. Or disease may be due to the invasion of the body by parasites, which rob the host of food, interfere with its water supply, or upset some necessary function. A study of diseases forms a great field in itself,

[1] *Loc. cit.* See reference, page 245.

plant pathology, under which name *therapeutics*, the study and application of remedial measures, is also usually comprehended. It is one of the divisions of botany which is of great economic importance, and one whose study has reached its highest level in this country, where the remedial and preventive measures devised save annually many millions of dollars. The knowledge of infectious diseases has been most extensively developed, but therein a great field for investigation still lies open, and a still greater one in the more difficult study of functional disorders.

Mechanical injury. — Mechanical injuries often lead to death, especially because they expose the plant to infection by bacteria and fungi. Unwise pruning of trees in our cities, much more the heedless hacking at the hands of linemen stringing telegraph and telephone wires, and the occasional barking of trees by careless auto drivers, frequently open the way for infection by some deadly parasite. Ice storms, hail, winds, and lightning all contribute to serious mechanical injuries at times, whose direct effects are less to be feared than the indirect.

Heat and cold. — High temperature is a fruitful cause of local death, for this is often associated with a deficiency in the water supply. There has been recognized a falling of the leaves, especially of trees, in midsummer, which is due to the heat, and may amount to a large per cent of the total foliage. The older leaves, and those least favorably situated for receiving sufficient water (the latter are at the same time most exposed to the direct rays of the sun) are the ones that suffer most. Low temperatures kill tender plants by direct injury to the protoplasts, even before the freezing point is reached. Others are killed only by the freezing itself, probably because this withdraws water from the protoplast and vacuoles, thus concentrating the solutions, perhaps to a point where certain solutes may become poisonous. There are many plants, however, which are able to withstand freezing, and on gradual thawing the water is taken back into the protoplast again. All the trees and shrubs and the persistent parts of herbaceous perennials are liable to be solidly frozen, often more than once, in the winters of the northern states and Canada, but they usually bear this unharmed, though the trees then have almost a maximum water content. The most serious danger in the northern winters, especially to the evergreens, is that during a warm period the evaporation will surpass the income from the shaded and frozen soil.

Temperature and water. — In general the proportion of water present determines the resistance to injury by low and high temperatures, other things being equal. Thus air-dry seeds withstand the lowest temperature yet tried, that of liquid hydrogen (− 250° C.),[1] and germinate freely when planted; while the same seeds, if soaked in water until swollen, will be killed by freezing at a very much higher temperature. In like manner temperatures short of absolute charring are borne by dry seeds, while a few minutes' exposure at 70° C. will kill soaked ones. Similarly, plants of firm texture and little sap withstand unfavorable temperatures better than watery ones. Even at room temperature, however, air-dry seeds seem to undergo a slow denaturing of the proteins that leads to ultimate death of the seeds. This slow denaturing of the embryo proteins probably sets a limit to the longevity of the seeds, and is probably in part a temperature effect.

Poisons. — Various substances, comprehensively known as poisons, kill the protoplasts, when their concentration is sufficient. Some of these have been considered in connection with the influence of external conditions on plant growth (see page 218). At lower concentrations many of the very same substances accelerate growth or development or special functions. The action of these substances may depend upon their dissociation in solution into ions, if they are electrolytes, or upon the molecules themselves, or both. Some act by coagulating the protoplasm and others induce changes of a different sort, not accurately known. Ionic hydrogen, silver, copper, and mercury are remarkably injurious. A solution of only one part per million of a silver salt is quickly fatal to the roots of lupines, and still less of mercury kills. Some very important economic measures depend upon the extreme sensitiveness of protoplasm to such substances. For microscopic study it makes possible the almost instant killing of the protoplasts, and by combining a fixing with the killing agent, the preserving of the protoplast in a form which approaches closely the condition in life; so far, at least, as can be judged from what can be seen of minute structures in the living condition. It must not be forgotten, however, that killing and fixing reagents always coagulate the colloids of the cell, and that in life the material of the coagulum is always in a dispersed state. Further, the poisonous nature of such substances makes it possible to employ them against the agents of infectious diseases,

[1] Doubtless they will endure the temperature of liquid helium (within a few degrees of the absolute zero, − 273° C.).

particularly those that grow on the surface of the host. The poisons act at lower dilutions upon the parasite, because its protoplasm is more accessible than that of the host, whose epidermis prevents injury in great measure. The usual form in which they are employed is in solution, which can be sprayed at appropriate times over the host. Many most destructive diseases are thus held in check. Where a disease is transmitted with the seed, they may be disinfected by short soaking in a suitable solution, such as copper sulphate, formaldehyde, or hyposulphites, without materially injuring their germinative power. Some of the organic compounds of mercury, like "uspulun" and "semesan," are quite useful in the disinfection of seeds. The modern methods of antiseptic surgery, personal and municipal hygiene, and the treatment of infectious diseases rest essentially upon like principles, for in nearly all these cases the organisms to be combated are plants.

The death of plants appropriately terminates a discussion of their behavior.

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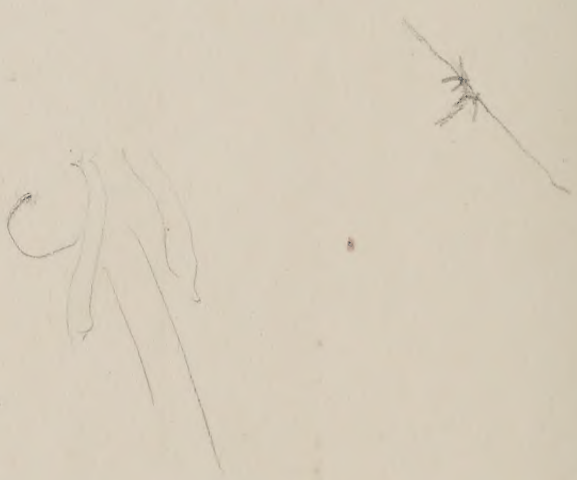

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